REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 14. POSTCRANIUM OF *SHOSHONIUS COOPERI* (MAMMALIA: PRIMATES)

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ABSTRACT

Postcranial elements of the omomyid primate *Shoshonius cooperi* are described from the late early Eocene (Lostcabinian) Buck Spring Quarries, Wind River Formation, central Wyoming. A complete right humerus, left femur, and nearly complete right tibia are among the remains. These allow several limb indices of functional importance to be estimated for the first time in the Omomyidae. Comparative functional analysis of the skeletal anatomy of *Shoshonius* indicates that leaping was an important part of its locomotor repertoire, but that *Shoshonius* was less specialized for leaping than is living *Tarsius* or those galagines classified as vertical clingers and leapers. Rather, *Shoshonius* more closely resembles cheirogaleids, *Otolemur*, and *Galagoides demidovii*, prosimian taxa in which quadrupedalism and climbing are as important components of the locomotor repertoire as is leaping. *Shoshonius* differs from specialized vertical clingers and leapers and resembles leaper-quadrupeds particularly in its relatively short, robust femur, high humerofemoral index, spherical humeral head, and long, low humeral trochlea. Although postcranial elements are known for only a small fraction of North American omomyids, *Shoshonius* closely resembles these taxa in most aspects of postcranial morphology, indicating that they too were likely more generalized than specialized in positional behavior.

Phylogenetic analysis of postcranial characters provides modest support for the monophyly of Tarsiiformes, which includes Eocene- Recent Tarsiidae, Eocene Omomyidae, and Eocene Microchoeridae. The hypothesis that tarsiids are more closely related to anthropoids than to Eocene omomyids and/or microchoerids requires much more homoplasy in the postcranial skeleton and is not supported by available evidence.

KEY WORDS: Eocene, Primates, Postcranium, *Shoshonius*

INTRODUCTION

From 1985 to 1991, field crews from the Carnegie Museum of Natural History collected 13 limb elements of an omomyid primate from the Buck Spring Quarries, Wind River Basin, Wyoming (Table 1). The specimens are late Lostcabinian in age, dating to roughly 50.5 Ma (Stucky et al., 1990; Beard et al., 1991). Although none of these omomyid postcranial elements was found in articulation or in direct association with craniodental remains, they are attributed here to *Shoshonius cooperi*, a species that is represented at this locality by numerous skulls, jaws, and teeth (Stucky et al., 1990; Beard et al., 1991; Beard and MacPhee, 1994). The bones are identified as omomyid on the basis of their great similarity

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Table 1.—*Postcranial elements of* Shoshonius cooperi *from the Buck Spring Quarries, Wind River Formation, Wind River Basin, Wyoming.*

Specimen	CM locality	Description
CM 67297	2404: K6, Quarry 6	left talus, complete
CM 67298	2404: K6, Quarry 6	left talus, virtually complete (slightly damaged posteroplantarly)
CM 67299	2404: K6, Quarry 6	right calcaneus, virtually complete (slightly damaged distomedially)
CM 69753	2409: K6, Quarry 11	left femur, proximal end (missing lesser trochanter)
CM 69754	2409: K6, Quarry 11	right metatarsal I, proximal end
CM 69755	2404: K6, Quarry 6	right humerus, complete
CM 69756	2404: K6, Quarry 6	left talus, complete
CM 69757	2404: K6, Quarry 6	right tibia, virtually complete (missing proximal end)
CM 69758	2404: K6, Quarry 6	left humerus, virtually complete but dorsoventrally crushed (missing distal part of supinator crest, capitulum)
CM 69759	3219: K6, surface	right tibia, distal end
CM 69760	2404: K6, Quarry 6	right femur, proximal end (missing lesser trochanter)
CM 69764	2404: K6, Quarry 6	left femur, complete (head slightly damaged)
CM 69765	2409: K6, Quarry 11	left calcaneus, complete

to homologous bones of other primates, especially omomyids. Their small size precludes assignment to Adapidae. Cranial and dental remains of *Shoshonius* far outnumber those of any other primate at this locality (Stucky et al., 1990). *Shoshonius* has traditionally been classified among the washakiin omomyines (Szalay, 1976; Honey, 1990). Among omomyids, *Shoshonius* is noteworthy because its cranial anatomy has been interpreted as evidence for a close phylogenetic relationship between this genus (and possibly other omomyids for which skulls remain unknown) and extant *Tarsius* (Beard et al., 1991; Beard and MacPhee, 1994).

Among the recovered postcranial elements are several virtually complete limb bones. Entire limb bones are extremely rare in the fossil record of tarsiiform primates, the only other examples being the nearly complete humeri, femora, and tibiofibulae of certain European microchoerids (Schlosser, 1907; Weigelt, 1933; Szalay and Dagosto, 1980; Dagosto, 1985; Dagosto and Schmid, 1996). The new material described here allows several limb indices of functional importance to be estimated for the first time in North American Omomyidae. Functional analysis of the postcranial anatomy of *Shoshonius* indicates that, although leaping was an important part of its locomotor repertoire, *Shoshonius* was not as anatomically specialized for this behavior as is living *Tarsius* or those galagines classified as vertical clingers and leapers (*G. senegalensis, G. moholi, G. gallarum*). Rather, *Shoshonius* most closely resembles those prosimian primates in which quadrupedalism and climbing are as important components of the locomotor repertoire as is leaping. This group of primates includes living cheirogaleids, *Galagoides demidovii*, and *Otolemur*. *Shoshonius* differs from specialized vertical clingers and leapers (VCLs) and resembles leaper/quadrupeds (LQs) in its relatively short, robust femur, high humerofemoral index, spherical humeral head, and long, low humeral trochlea.

Institutional acronyms are as follows: CM, Carnegie Museum of Natural History (Pittsburgh, Pennsylvania); FMNH, Field Museum of Natural History (Chicago, Illinois); UCMP, University of California Museum of Paleontology (Berkeley, California); USNM, National Museum of Natural History (Washington, D.C.).

ANATOMY OF *SHOSHONIUS COOPERI*

The limb bones of *Shoshonius* were compared with those of small prosimian primates, particularly cheirogaleids, galagos, and tarsiers, as well as those of other omomyids. Measurements of postcranial elements of *Shoshonius* are provided in Table 2. Definitions of limb measurements (and indices derived from these measurements) are provided by Szalay and Dagosto (1980), McArdle (1981), Dagosto (1985), Gebo (1988), Gebo et al. (1991), Dagosto and Schmid (1996), and Schmitt (1996).

Body Size.—The limb elements of *Shoshonius* are comparable in size to those of *Microcebus* and *G. demidovii* (50–70 g), but are much smaller than those of *Tarsius* (100–130 g) (Bearder, 1987; Rickart et al., 1993) (Table 3; Fig. 1). This suggests a body weight for *Shoshonius* well below estimates based on molar size, which range from 103–122 g (Conroy, 1987) to 155 g (Fleagle, 1988). Instead, regression equations based on postcranial dimensions (Table 4) suggest a body weight for *Shoshonius* conservatively estimated at 60–90 g. This discordance between weight estimates based on teeth and postcranial elements is common among omomyid primates (Dagosto and Terranova, 1992), and indicates relative megadonty in these small animals.

Limb Indices.—The humerofemoral index (HFI) of *Shoshonius* calculated from the mean of the two humeri (CM 69755 and CM 69788) and the single femur (CM 69764) is 64.6. Calculating the HFI separately for each humerus yields values of 63.3 and 65.9. These long bones are probably not all derived from the same individual. However, these values are very reasonable approximations of HFI in *Shoshonius* for the following reasons. (1) The probability of mixing long bones from two omomyid species of different body size is extremely low, because other omomyids are rare at this site (Stucky et al., 1990). (2) The size range observed in the skulls, dentitions, and limb bones of *Shoshonius* indicate that there was not a great degree of intraspecific variation in size. (3) The correlation between species mean HFI and HFI estimated from mean humerus length and mean femoral length is high ($r = 0.997$) in a sample consisting of 13 species of galagos, cheirogaleids, and tarsiers (Table 5). (4) In extant species with low HFIs, one cannot derive an HFI as high as that of *Shoshonius*, even if the index is constructed using the shortest femur and the longest humerus (Table 5). Conversely, in species with high HFIs, one cannot derive a particularly low HFI, even if the shortest humerus and longest femur are compared. (5) Finally, HFIs were constructed by having the computer randomly select a humerus and a femur from each species sample 100 times and averaging the values. The values obtained were not significantly different from the mean species HFI.

An HFI of 64.6 is quite high compared to specialized VCL primates (*Tarsius, Galago*: HFI 45–50), but similar to the proportions of the more frequently quadrupedal galagos (*Otolemur, Galagoides*) and cheirogaleids (Table 6). Figure 2 shows the disparity in humerofemoral lengths in *Tarsius* and *Shoshonius* (see Figure 1 for a comparison of *Shoshonius* and *Microcebus*). The estimated HFI of *Microchoerus* is 59 (Dagosto, 1993), indicating a greater degree of hind-limb dominance in this microchoerid than in *Shoshonius*.

The HFI is highly correlated ($r = 0.977$) with the intermembral index (IMI) in a sample composed of galagos, tarsiers, and cheirogaleids (although this may not be the case among primates generally; Jungers, 1985). This allows the intermem-

Table 2.—*Measurements (in mm) of postcranial elements of* Shoshonius cooperi.

Element: dimension	Specimen			Mean
	CM 69755	CM 69758		
Humerus	CM 69755	CM 69758		
length	24.87	23.90		24.39
proximal width	4.11	4.19		4.15
proximodistal chordal length of head	3.49	3.16		3.33
inferior mediolateral width of head	2.97	2.83		2.90
length of deltopectoral crest	10.03	9.50		9.77
anteroposterior width of midshaft	1.94			1.94
mediolateral width of midshaft	1.98			1.98
width of trochlea	2.03	2.26		2.15
height of trochlea	1.56	1.70		1.63
width of capitulum	1.40			1.40
width of capitulum + tail	1.93			1.93
width of distal articular surface	4.29			4.29
width of medial epicondyle	2.15	1.75		1.95
bicondylar width	6.12			6.12
length of brachial flange	10.00	9.22		9.61
Femur	CM 69764	CM 69760	CM 69753	
length	37.76			37.76
breadth of shaft distal to lesser trochanter (BSDLT)[1]	2.59	2.36	2.31	2.42
neck length 1[1]		3.63	3.93	3.78
neck length 2[1]	2.17	1.57	1.60	1.78
neck angle, in degrees[1]	70	63	68	67
fossa length[1]	2.50	3.04	2.97	2.84
width of lesser trochanter	2.00			2.00
height of lesser trochanter[1]	3.27			3.27
height of third trochanter[1]	1.62	2.42	2.38	2.14
width of third trochanter	1.34	1.19	1.16	1.23
anteroposterior width of midshaft	2.15			2.15
mediolateral width of midshaft	2.46			2.46
height of lateral condyle	5.63			5.63
bicondylar width	5.05			5.05
Tibia	CM 69757	CM 69759		
length (estimate)	38.00			38.00
height of cnemial crest	3.49			3.49
anteroposterior width of midshaft	2.04			2.04
mediolateral width of midshaft	1.90			1.90
length of distal facet	2.74	2.99		2.87
width of distal facet	2.33	2.57		2.45
malleolar rotation, in degrees	18	13		15.5
Talus	CM 67297	CM 67298	CM 69756	
length (A1)[2]	5.24	5.66	5.66	5.52
width (A2)[2]	2.66	2.90	2.84	2.80
neck length (A5)[2]	2.75	3.12	2.81	2.89
length of trochlea (A3)[2]	2.66	2.78	2.64	2.69
width of trochlea (A4)[2]	2.04	2.01	2.09	2.05
lateral height (A7)[2]	2.37		2.37	2.37
width of head	1.87	1.94	2.20	2.00
height of head	1.84	1.81	1.60	1.75
Calcaneus	CM 69765	CM 67299		
length (C1)[2]	9.82	9.76		9.79
width (C2)[2]	2.97	3.53		3.25

Table 2.—Continued.

Element: dimension	Specimen		Mean
	CM 69755	CM 69758	
length of posterior talocalcaneal facet (C3)^2	2.27	2.18	2.23
width of posterior talocalcaneal facet (C4)^2	1.37	1.13	1.25
heel length (C7)^2	2.15	2.28	2.22
anterior length	5.00	5.19	5.10
width of cuboid facet (C6)^2	2.29	2.34	2.32
height of cuboid facet (C5)^2	1.56	1.53	1.55

[1] See Dagosto and Schmid (1996) for explanation of measurements of the proximal femur.
[2] See Dagosto and Terranova (1992) for explanation of tarsal measurements.

Table 3.—Measurements (in mm unless noted otherwise; species means are given) of postcranial elements in Shoshonius and some extant prosimians. See Dagosto and Terranova (1992) for definition of tarsal measurements used here.

Measure	Shoshonius cooperi	Microcebus murinus	Galagoides demidovii	Tarsius syrichta	Galago moholi	Galago senegalensis	Cheirogaleus medius
weight, in g	?	50	70	125	160	215	233
area of M_1, in mm^2	3.40	2.22	3.37	7.01	4.11	4.83	4.87
area of M^1, in mm^2	5.25	3.70	5.50	11.69	7.30	8.02	6.37
Talus							
A1	5.52	5.46	5.54	6.73	8.01	8.37	6.62
A2	2.80	2.71	3.40	4.13	5.11	5.38	3.84
A3	2.69	2.49	2.94	3.93	4.31	4.18	3.62
A4	1.97	1.85	2.10	3.13	3.28	3.28	2.60
Calcaneus							
C1	9.79	9.87	21.05	26.10	28.19	29.82	9.88
C2	3.25	2.52	3.05	3.58	4.33	4.70	3.58
C3	2.25	1.85	2.24	3.15	3.29	3.47	2.88
C4	1.25	1.17	1.35	1.70	2.18	2.13	1.68
C5	1.55	1.68	1.90	2.30	2.43	3.00	2.10
Humerus							
length	24.38	20.89	25.64	28.38	31.27	32.10	27.01
anteroposterior width of midshaft	1.89	1.70	1.79	2.30	2.51	2.69	2.57
mediolateral width of midshaft	1.98	1.71	1.61	2.12	2.47	2.69	2.55
bicondylar width	6.12	4.92	5.76	7.91	8.12	8.53	8.29
Tibia							
length	38.00	33.40	42.38	57.13	57.52	60.38	40.50
Femur							
length	37.76	29.41	38.39	56.65	62.83	68.10	39.90
anteroposterior width of midshaft	2.15	2.00	2.16	2.76	3.81	4.38	2.78
mediolateral width of midshaft	2.46	3.14	2.05	2.43	3.18	3.68	2.76
bicondylar width	5.05	4.47	4.55	6.10	7.30	7.74	7.37

Fig. 1.—Postcranial elements of *Shoshonius cooperi* (left of each pair) compared with those of *Microcebus murinus* (right of each pair).

bral index of *Shoshonius* to be estimated as 66 (95% confidence intervals = 64–68).

McArdle (1981) ranked galagos into three groups based on the IMI. Those with the highest IMI (> 66) (*Otolemur, G. demidovii*) use quadrupedalism most frequently; the intermediate group (IMI = 62–64: *Euoticus, G. alleni, G. zanzibaricus*) uses quadrupedalism less frequently; and the third group (IMI < 60: *G. moholi, G. senegalensis, G. gallarum*) includes the most frequent leapers. This scheme works fairly well for other prosimians as well. Cheirogaleids, most lemurids, and *Daubentonia* fall into group 1; *Hapalemur, Lepilemur*, and most indriids in group 2; and tarsiers and *Avahi* in group 3. Distribution of these taxa on the basis of HFI follows an identical pattern. *Shoshonius* falls at the junction of groups 1 and 2, with the leaper/quadrupedal forms, not the most specialized leapers.

The humerotibial index (HTI) of *Shoshonius* is estimated at 64. The distribution of this index is quite similar to that of the HFI and IMI, and thus *Shoshonius* again groups with the non-VCL forms. The HTI of *Necrolemur* is estimated at 53 (Dagosto, 1993), which is lower than *Shoshonius*, but still higher than in extant VCL forms.

The crural index of approximately 100 is typical for prosimians (Table 6). This index shows few correlations with locomotor groups, but *Shoshonius* likely did not have the unusually high crural index of *G. demidovii* or *Microcebus*. Given its humerus length of roughly 24 mm, the unknown radius of *Shoshonius* would have been unusually long to achieve a brachial index greater than 100, values that are typical for tarsiers and indriids (but not galagos).

Table 4.—*Estimation of body mass (in g) of* Shoshonius cooperi *derived from dental and postcranial measures. Prediction equations are based on least squares regression of a strepsirhine dataset. Sources of equations used to predict body mass are as follows:* [1] Dagosto and Terranova (1992); [2] Conroy (1987); *and* [3] Terranova (1994).

Measure	Mean predicted body mass	95% confidence intervals (lower–upper)
M^1 area[1]	113	77–165
M_1 area[1,2]	120, 103	92–158
humerus length[3]	69	
anteroposterior width of humeral midshaft[3]	64	
mediolateral width of humeral midshaft[3]	73	
femur length[3]	72	
anteroposterior width of femoral midshaft[3]	60	
mediolateral width of femoral midshaft[3]	106	
A1[1]	90	84–96
A2[1]	61	57–66
A3[1]	66	62–70
A4[1]	72	67–77
A7[1]	84	79–89
C2[1]	121	115–128
C3[1]	97	91–103
C4[1]	53	49–58
C5[1]	50	45–55
C6[1]	102	97–107
C7[1]	107	94–122
Index 1[1]	83	78–88
Index 4[1]	69	65–73
Index 6[1]	69	65–74
minimum	50	45–55
maximum	121	115–128
mean	78	75–86

Table 5.—*Estimation of the humerofemoral index (HFI) in some extant prosimians.*

Locomotor category/taxon	Species mean HFI	mean humerus/ mean femur	shortest humerus/ longest femur	longest humerus/ shortest femur	randomly generated HFI
Specialized leapers					
Tarsius bancanus	45.9	45.7	42.9	51.1	45.5
Galago senegalensis	47.1	47.1	40.5	53.4	48.0
Galago gallarum	49.0	48.1	43.1	54.2	47.4
Galago moholi	49.6	49.6	43.4	54.6	50.1
Tarsius syrichta	50.8	50.1	42.0	61.0	49.4
Intermediates					
Euoticus elegantulus	59.1	58.8	53.8	69.4	59.2
Galago alleni	60.1	60.0	57.7	62.3	60.1
Leaper/Quadrupeds					
Otolemur garnetti	64.1	64.0	54.7	75.6	64.1
Cheirogaleus medius	65.8	65.8	62.0	69.6	65.8
Otolemur crassicaudatus	66.1	66.0	60.5	76.4	65.4
Galagoides demidovii	66.6	66.5	58.4	79.0	66.7
Microcebus murinus	71.1	71.0	56.3	90.0	71.2
Cheirogaleus major	71.4	71.5	53.3	92.4	70.8

Table 6.—*Limb indices in* Shoshonius cooperi *and some extant prosimians. Humerofemoral index (HFI) = (100)(humerus length)/femur length; intermembral index (IMI) = (100)(humerus length + radius length)/(femur length + tibia length); crural index (CI) = (100)(tibia length)/femur length; brachial index (BI) = (100)(radius length)/humerus length.*

Locomotor category/taxon	n	mean HFI, s.d.	mean IMI, s.d.	mean CI, s.d.	mean BI, s.d.
Shoshonius cooperi	1	64.6	~66	~100	?
Leaper/quadrupeds					
Microcebus murinus	19	71, 1.19	71, 0.95	112, 4.36	111, 5.88
Cheirogaleus medius	6	68, 2.7	68, 0.09	101, 1.7	103, 1.5
Cheirogaleus major	9	71, 2.41	70, 1.09	101, 2.96	98, 4.89
Otolemur crassicaudatus	9	66, 1.84	71, 0.59	95, 1.96	106, 2.28
Otolemur garnetti	10	64, 1.68	67, 1.39	94, 2.08	103, 4.73
Galagoides demidovii	12	66, 2.25	67, 0.7	109, 2.98	113, 2.38
Specialized leapers					
Galago moholi	9	50, 1.25	53, 0.35	91, 0.94	106, 3.13
Galago senegalensis	6	47, 0.56	53, 2.03	89, 0.79	103, 0
Galago gallarum	4	49, 1.6	51, 1.21	95, 0.71	103, 1.07
Tarsius syrichta	11	51, 0.88	57, 0.71	101, 1.39	126, 1.47
Tarsius bancanus	8	46, 2.19	52, 0.25	99, 0.84	126, 3.97

In summary, the new postcranial elements show that *Shoshonius* likely did not have the low HFI and IMI, nor the high brachial index typical of extant specialized vertical clingers and leapers, but was more comparable to less specialized leaper/quadrupeds in its limb proportions.

Limb Scaling.—The relationship between body mass and limb length in primates has been studied by several investigators (Jungers, 1985; Terranova, 1994). Assuming *Shoshonius* followed the scaling relationships of extant cheirogaleids, limb lengths yield body mass estimates higher than what most other postcranial dimensions would suggest (Table 7). Galagid equations yield reasonable weight estimates from humerus length, but low estimates from femur length. These observations suggest that *Shoshonius* likely had longer humeri and femora than would be expected in a cheirogaleid of its mass, while its femur was shorter than that of a comparably sized galago.

Another way to examine this is to predict long-bone lengths for *Shoshonius* assuming body weights of 60–100 g (Table 7). Humerus length is better predicted by the galago than the cheirogaleid equation; the cheirogaleid model grossly underestimates femur length, while the galago equation overestimates femur length. The relationship between body mass and humerus and femur length in *Shoshonius* does not appear to be significantly different from the average for strepsirhine primates. *Shoshonius* does not have the extremely elongated hind limbs typical of specialized leapers.

Humerus.—CM 69755 is the only complete humerus known from a North American omomyid (Fig. 3). It exhibits minor breakage along the deltopectoral crest and has eroded areas on the humeral head. Cracks run through the shaft and brachial flange. In a second specimen (CM 69758), the proximal part of the shaft is crushed, and the capitulum, lateral epicondyle, and lateral half of the brachial flange are missing.

The humeral head extends slightly above the greater tuberosity. The head is relatively round, being only moderately taller than wide (inferior width to prox-

Fig. 2.—Femur and humerus of *Tarsius* (left) and *Shoshonius* (right), scaled to the same humeral length. Note the greater relative length of the femur in *Tarsius*.

imodistal length index, Table 8; Fig. 4), and thus is more similar in shape to quadrupedal primates than to specialized vertical clingers and leapers, which have narrower humeral heads with limited mediolateral mobility distally (Schmitt, 1996). VCL primates also increase the range of flexion and extension possible at the shoulder joint by inflating the anterior-posterior dimensions of the humeral head (Schmitt, 1996). Our estimate of this feature (Table 8:ap extension index) indicates that *Shoshonius* again groups with the leaper/quadrupeds, not the specialized VCLs. In contrast, *Microchoerus* exhibits a narrower, anteroposteriorly extended humeral head similar to that of VCL primates.

The attachment areas for the shoulder muscles are better developed in *Shoshonius* than in most extant prosimians (Fig. 1–4). The lesser tuberosity is prominent, as is the attachment area for latissimus dorsi. The deltopectoral crest comprises 40% of the total length of the humerus, which is typical for extant primates, and is quite extensive anteriorly. The brachial flange, the area for attachment of the brachial and brachioradialis muscles, is also prominent and curves back along the shaft proximally. The flange covers 39% of the length of the humerus. The

Table 7.—*Scaling of body mass (in g) and humerus and femur length (in mm) in* Shoshonius cooperi. *Sources of equations used to predict body mass are as follows:* [1] *Terranova (1994);* [2] *Jungers (1985).*

Element/scaling model	Actual value	Predicted weight	Predicted limb length at 60 g	Predicted limb length at 80 g	Predicted limb length at 100 g
Humerus	24.38				
Cheirogaleid model					
length/mass[1]		111.7	13.4	15.9	18.1
length/mass[2]		112.9	18.8	21.2	23.1
Galagine model					
length/mass[1]		80.8	22.3	24.7	26.8
length/mass[2]		68.9	23.1	25.6	27.7
Strepsirhine model					
length/mass		69.3	23.2	25.6	27.7
Femur	37.76				
Cheirogaleid model					
length/mass[1]		126.6	18.8	22.3	25.5
length/mass[2]		143.2	26.2	29.5	32.4
Galagine model					
length/mass[1]		52.0	51.7	54.8	57.3
length/mass[2]		45.8	41.1	45.1	48.4
Strepsirhine model					
length/mass		72.8	35.2	39.1	42.3

lateral extent of the flange is similar to that of many prosimian primates, including *Tarsius*, but is wider than in *Microchoerus*.

The capitulum is very round and ball-like compared to the more proximodistally elongated, mediolaterally restricted capituli of *Absarokius* and *Hemiacodon* (Fig. 5). In this feature, *Shoshonius* is more like *Tarsius* than are other omomyids. *Shoshonius* has a capitular tail that is similar in relative length to a variety of prosimian primates (Gebo et al., 1994). As in other omomyids the trochlea is long
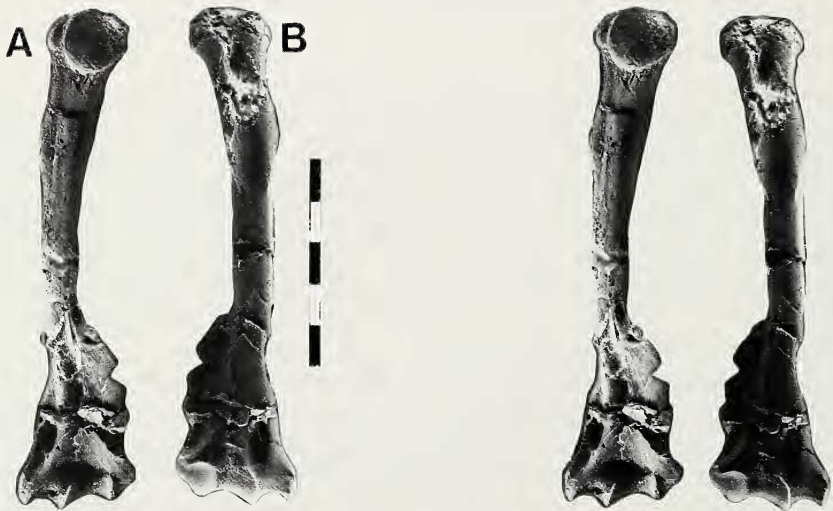
Fig. 3.—Right humerus of *Shoshonius cooperi* (CM 69755) in posterior (A) and anterior (B) views. Both views are stereopairs. Scale = 10 mm.

(47% of articular width), and lower (76% of trochlear length) than in extant vertical clingers and leapers. Thus, the elbow joint of *Shoshonius* is more similar to that of leaper/quadrupeds (Szalay and Dagosto, 1980). As in other haplorhines, the trochlea is downturned (i.e., the medial edge extends further distally than does the lateral edge). A large entepicondylar foramen is present. The medial epicondyle is broad and medially directed, and thus does not differ from the configuration typical of most prosimian primates, including other omomyids. Posteriorly, the olecranon fossa is shallow, with low crests running along the rims of the trochlea. A shallow dorsoepitrochlear fossa is present as in other omomyids and microchoerids. *Tarsius* lacks this fossa. *Shoshonius* lacks the distally tapered, anteroposteriorly extended humeral head and high, short humeral trochlea typical of extant vertical clingers and leapers. The humerus is quite similar to that of less specialized leaper/quadrupeds, except for having more prominent muscle scars.

Femur.—CM 69764 is the most nearly complete femur ever recovered of an omomyid primate (Fig. 6). The head is damaged, especially medially, the shaft is cracked in several places, and the greater trochanter, lateral condyle, and patellar facet are slightly eroded. The head is well preserved in two other proximal femora (CM 69753 and CM 69760).

As in other omomyids, tarsiers, and galagos, the joint surface of the femoral head is extended onto the posterodorsal aspect of the femoral neck, and the posterior surface of the head is slightly flat (Fig. 7). Like *Hemiacodon* and other North American omomyids, the femoral head is only moderately flat medially and somewhat rounded dorsally. This semicylindrical shape of the femoral head in *Shoshonius* and *Hemiacodon* contrasts with the more fully cylindrical shape observed in galagos and tarsiers. The femoral neck and head are aligned to the shaft at an angle of 67° (Table 9), which is slightly less perpendicular than observed in other omomyids, galagos, or tarsiers. The neck is also relatively longer than in other North American omomyids, galagos, or tarsiers, but still fairly short compared to lemurids, indriids, and platyrrhines.

The entire proximal part of the femur is bowed anteriorly relative to the shaft. The greater trochanter overhangs the anterior part of the shaft and extends slightly proximal to the head. The anterior region of the proximal femur possesses an especially prominent lateral pillar extending from the greater trochanter, forming a central triangular fossa on the proximoanterior surface of the femur for the attachment of vastus lateralis. In all of these features, *Shoshonius* resembles other omomyids and tarsiers. The lesser trochanter is fairly broad (high projection index) and protrudes from the shaft at an angle of 30°, which is a more posterior orientation than in other omomyids, galagos, or tarsiers. *Necrolemur* resembles *Shoshonius* in terms of orientation of the lesser trochanter. The third trochanter is laterally prominent, and more similar in its size, morphology, and placement to *Tarsius* and other omomyids than to galagos, in which the third trochanter is incorporated into a crest extending distally from the greater trochanter (Burr et al., 1982; Dagosto and Schmid, 1996). The third trochanter is proximal to the lesser trochanter. A paratrochanteric crest is present. The trochanteric fossa is deep but short as in other omomyids (and in contrast to *Necrolemur*), although not quite as short as in galagos or tarsiers. There is no intertrochanteric crest.

The robusticity of the femoral shaft of *Shoshonius* is more comparable to leaper/quadrupeds than to specialized leapers, and is likely an additional reflection of a relatively short femur in this omomyid. In contrast to most extant strepsirhines and *Tarsius* (except *Otolemur crassicaudatus* and some cheirogaleids; Terranova,

Table 8.—Indices of the humerus in Shoshonius cooperi, other fossil tarsiiforms, and some extant prosimians. Mean values are provided first, with ranges in parentheses. Abbreviations are as follows: N (x,y), sample sizes of proximal and distal humeri, respectively; INFW, width of inferior quadrant of humeral head; PD CHORD, proximodistal chordal length of humeral head; AP EXT, central anteroposterior chord from PD CHORD/INFW; DPCL, maximum deltopectoral crest length; HL, humerus length; BFL, brachial flange length; TH, trochlear height; TW, trochlear width; AW, width of distal articular surface of humerus; CTW, capitular tail width; CW, capitular width. Humeral head measurements after Schmitt (1996); due to the small size of Shoshonius, the same method of measuring could not be adopted. Instead, PD CHORD (corresponds to Schmitt's measurement PD central) and INFW (corresponds to Schmitt's measurement ML inf) were measured directly from the specimens with calipers. AP EXT was measured by tracing the proximodistal arc of the humeral head with a camera lucida, and measuring the perpendicular distance from the highest point of the arc to the implicit PD CHORD (corresponds to Schmitt's measurement AP cent). Distal humerus measurements after Szalay and Dagosto (1980) and Gebo et al. (1994). Absarokius data are from Covert and Hamrick (1993).

Taxon	N (x,y)	Humeral head		Humeral shaft			Elbow joint	
		INFW/PD CHORD	AP EXT	DPCL/HL	BFL/HL	TW/AW	TH/TW	CTW/CW
Shoshonius cooperi	2, 1	87.3 (85.1–89.6)	56.7 (55.8–57.6)	40 (39.7–40.3)	39.4 (38.6–40.2)	47.3	76 (75.2–76.8)	37.8
Hemiacodon gracilis	0, 3					45.8 (42.9–47.8)	69.2 (67.8–73.8)	33.5 (29.4–37.6)
?Tetonius (UCMP)	0, 1					35.4	78.2	
UCMP 113301	0, 1					44.3	61.9	
Absarokius	0, 1					42.4	70.7	28.4
Necrolemur sp.	0, 2					49.1 (47.1–51.2)	81.2 (79.0–83.5)	46.6 (46.0–47.2)
Microchoerus sp.	1, 2	72.5	84.5	46.2	39.1	49.0 (47.1–50.8)	70.2 (68.0–72.4)	38
Leaper/quadrupeds								
Microcebus murinus	6, 18	73.4 (70.6–77.0)	71.4 (65.2–79.0)	41.8 (39.4–45.5)	36.1 (32.1–38.4)	48.4 (43.5–55.2)	77 (66.7–85.8)	25.6 (22.5–25.6)
Cheirogaleus medius	3, 3	75.8 (70.1–81.9)	62.5 (58.3–66.8)	46.4 (45.4–48.4)	39.5 (36.0–43.5)	49.8 (44.4–53.8)	77.8 (64.1–88.7)	
Cheirogaleus major	2, 6	80.7 (73.7–87.8)	71.8 (69.5–74.1)	43.2 (42.2–44.3)	43.1 (42.4–43.9)	46.4 (43.2–50.0)	78.3 (71.0–92.5)	58.2 (44.5–72.0)
Otolemur crassicaudatus	3, 7	77.0 (74.9–79.0)	57.4 (54.1–60.6)	41.9 (40.8–42.4)	37.8 (35.5–39.5)	44.8 (41.8–48.9)	90.1 (82.7–102.1)	42.2 (41.7–42.7)
Otolemur garnetti	3, 6	74.2 (64.6–81.2)	64.6 (47.7–83.6)	42.7 (41.0–44.8)	38.3 (35.6–39.9)	44.1 (42.0–47.8)	81.7 (74.1–95.9)	41.1 (33.3–48.8)
Galagoides demidovii	4, 7	70 (66.6–74.1)	76 (69.7–77.9)	39.7 (36.5–40.9)	41.5 (34.4–44.7)	45.0 (41.2–49.2)	91.7 (78.4–101.5)	

Table 8.—*Continued.*

| Taxon | N (x,y) | Humeral head | | Humeral shaft | | | | Elbow joint | |
		INFW/PD CHORD	AP EXT	DPCL/HL	BFL/HL	TW/AW	TH/TW	CTW/CW
Specialized leapers									
Galago moholi	6, 7	68	84.6	40.1	43.3	44.6	99.1	
		(62.7–73.5)	(77.7–98.1)	(37.8–43.2)	(41.9–45.6)	(42.8–45.4)	(93.8–105.5)	
Galago senegalensis	2, 2	69.0	70.4	41.1	47.9	36.2	109.2	48.7
		(68.7–69.3)	(68.1–72.8)	(40.3–41.8)	(47.4–48.5)	(33.4–39.0)	(108.7–109.7)	(45.9–51.5)
Galago gallarum	5, 5	65.6	92.8	42.5	43.2	41.8	103.3	
		(62.2–70.4)	(80.6–102.3)	(41.5–42.9)	(41.5–45.9)	(39.2–44.7)	(91.4–121.0)	
Tarsius syrichta	6, 10	70.6	81.7	38.8	34	41.9	101.9	39.3
		(62.6–77.3)	(73.3–82.0)	(33.4–41.9)	(31–37)	(37.8–47.9)	(86.5–121.0)	(17.2–53.3)
Tarsius bancanus	7, 6	66	86	40.1	38	38.4	113.4	41
		(59.3–76.3)	(75.6–115.8)	(32.9–44.4)	(34–44)	(33.3–43.7)	(96.6–135.1)	(16.5–70.0)

Fig. 4.—Proximal humeri of extant prosimians (top) and *Shoshonius* (bottom), all in posterior view. From left to right, extant taxa are as follows: *Tarsius syrichta* (FMNH 129379), *Cheirogaleus medius* (FMNH 85146), and *Galago senegalensis albipes* (FMNH 153087). Note the relatively narrower distal part of the humeral head in *Tarsius* and *Galago* compared to *Cheirogaleus* and *Shoshonius*. Scale in mm.
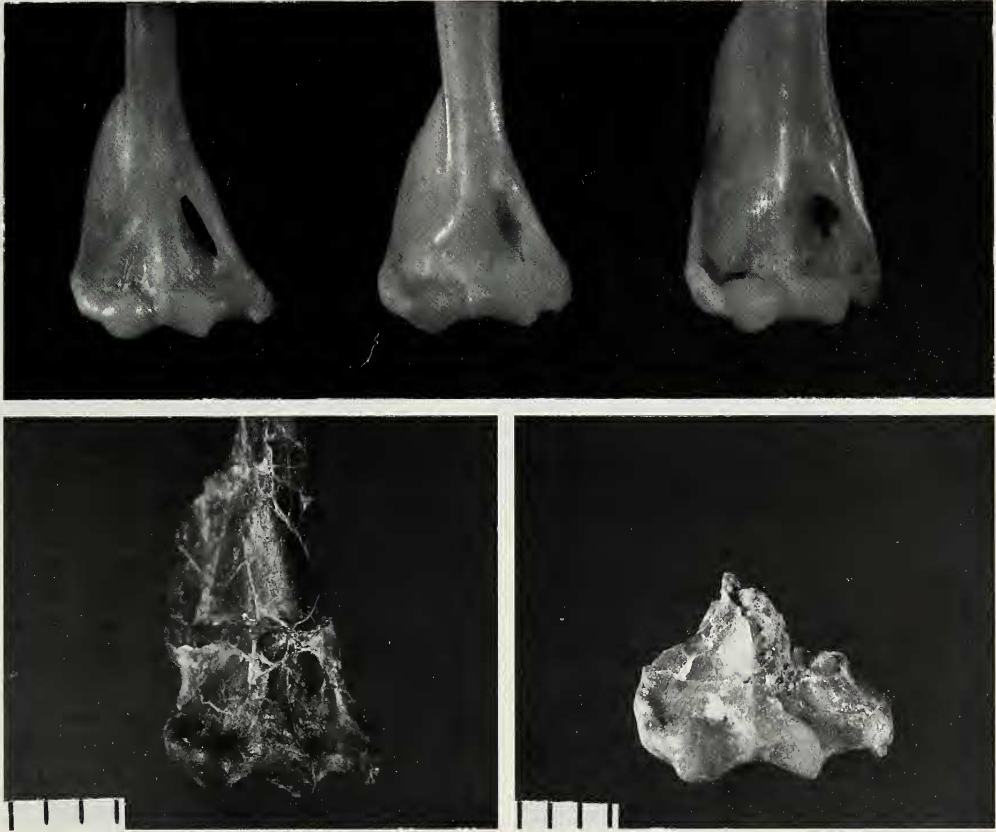
Fig. 5.—Distal humeri of extant prosimians (top) and Eocene omomyids (bottom), all in anterior view. From left to right, extant taxa are as follows: *Tarsius, Cheirogaleus,* and *Galago senegalensis.* Eocene omomyids are *Shoshonius cooperi* (left, CM 69755) and *Hemiacodon gracilis* (right, AMNH 126722). Note that the trochlea is relatively longer in *Shoshonius* and *Hemiacodon* than in *Tarsius* and that the capitulum is more spherical in *Shoshonius* and *Tarsius* than in *Hemiacodon.* Scale in mm.

1994), in *Shoshonius* the external mediolateral diameter of the femoral midshaft exceeds the anteroposterior diameter. *Otolemur crassicaudatus* and *O. garnettii* also have relatively lower ratios of ap to ml bending strength than other galagos (Demes and Jungers, 1993; Terranova, 1994). This suggests that in *Shoshonius,* the femur was not subjected to the high anteroposterior bending moments experienced by specialized leapers (Schaffler et al., 1985).

Specialized leapers are also distinguished by humeral/femoral contrasts in bone cross-sectional properties (Schaffler et al., 1985; Ruff and Runestad, 1992; Demes and Jungers, 1993; Terranova, 1994). Contrasts of external dimensions parallel the observed differences in bone cross-sectional properties. An index of humeral to femoral midshaft areas (external ap dimension multiplied by the ml dimension; Table 9) shows that specialized leapers (with the exception of *Tarsius*) have low indices (femoral area greatly exceeds humeral area), while leaper/quadrupeds have higher indices. The index of *Shoshonius* is higher than is usual in the specialized leapers, and more comparable to the leaper/quadruped group.

The knee is very tall and narrow, with an elevated and rounded lateral patellar
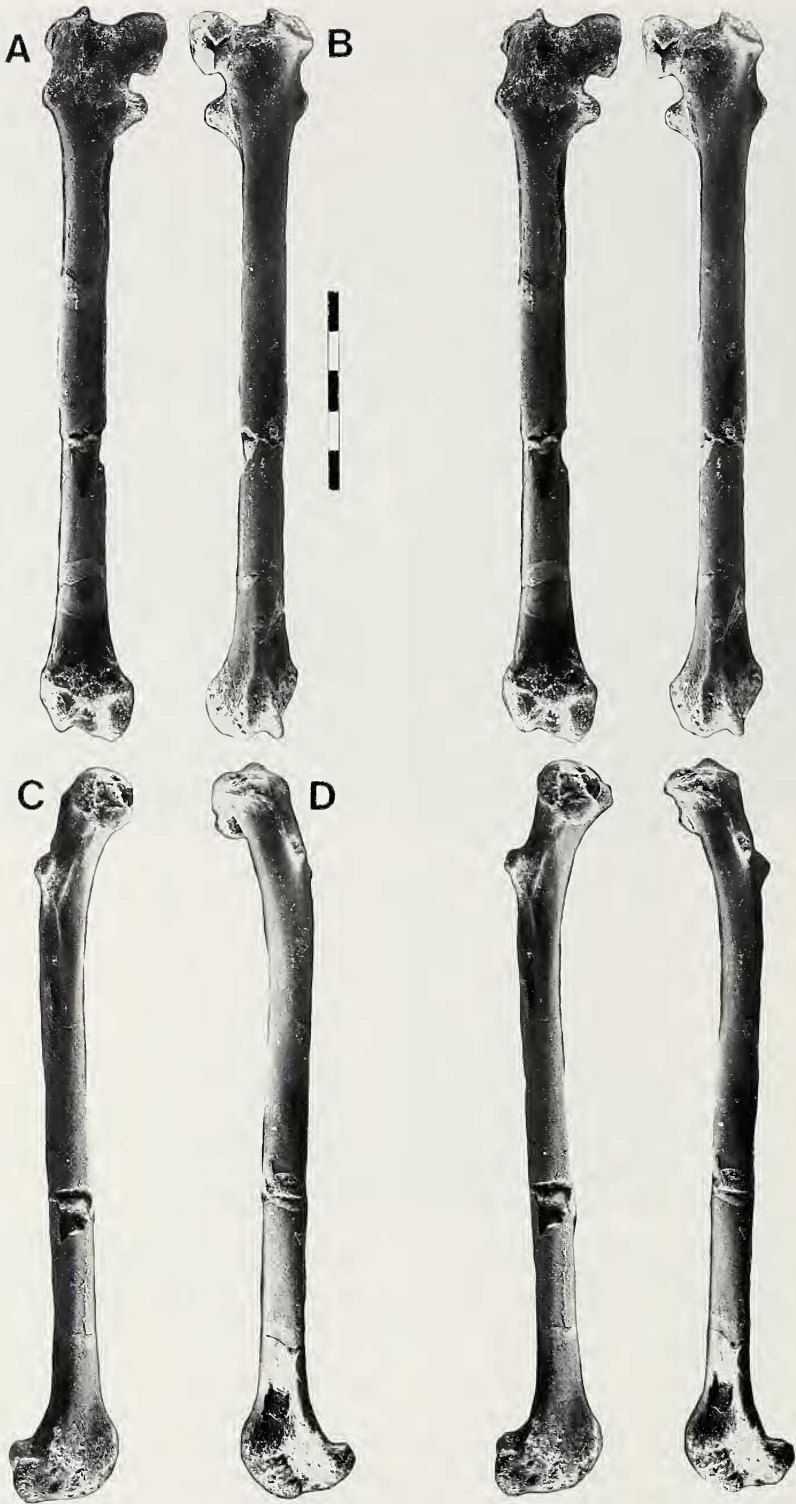
Fig. 6.—Left femur of *Shoshonius cooperi* (CM 69764) in posterior (A), anterior (B), medial (C), and lateral (D) views. All views are stereopairs. Scale = 10 mm.
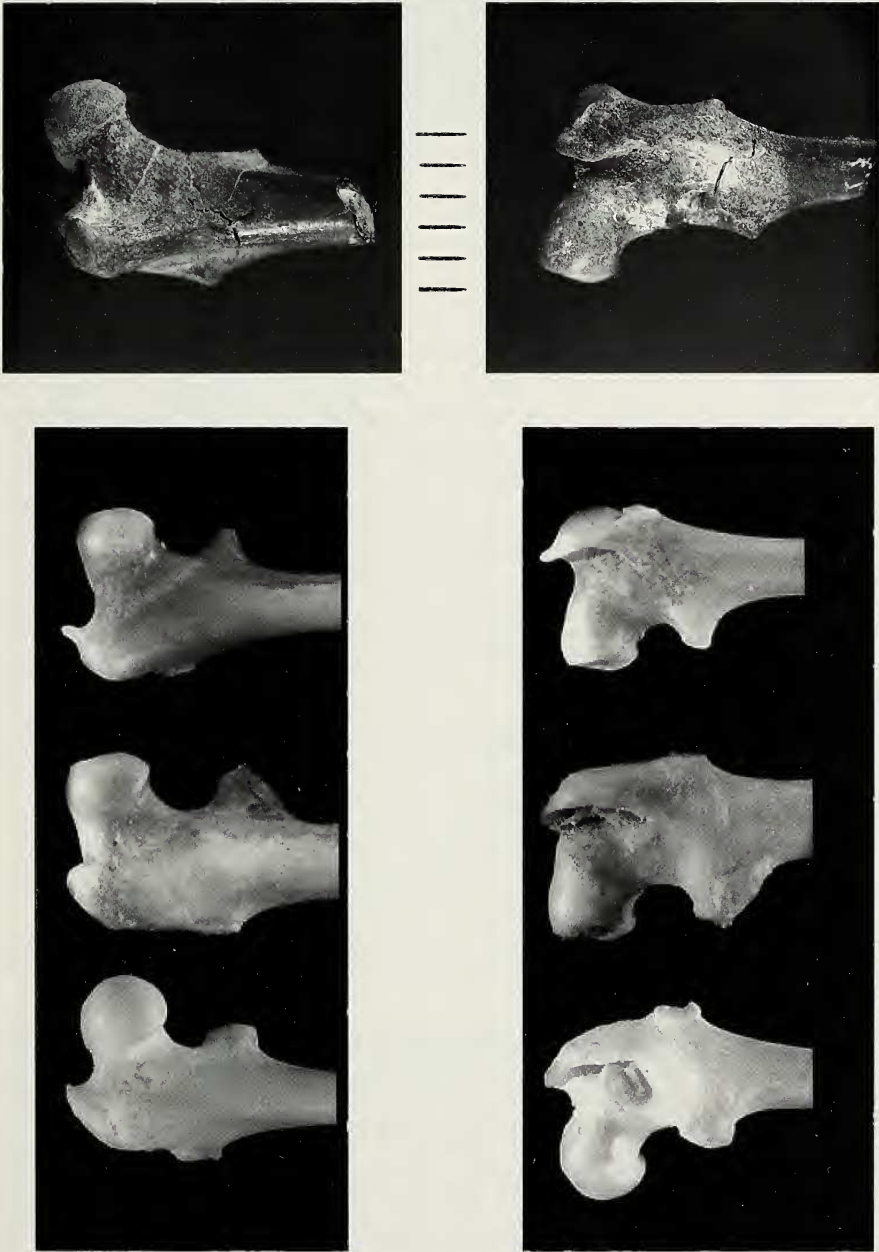
Fig. 7.—Proximal femora of extant prosimians and *Shoshonius* in anterior (top) and posterior (bottom) views. From left to right, specimens illustrated are as follows: *Cheirogaleus major* (FMNH 85144), *Otolemur ?garnetti* (FMNH 53066), *Tarsius syrichta* (FMNH 142007), and *Shoshonius cooperi* (CM 69760). Note the nearly spherical shape of the femoral head in *Cheirogaleus*, the semicylindrical shape of the femoral head in *Shoshonius*, and the more fully cylindrical shape of the femoral head in galagos and tarsiers. Scale in mm.

Table 9.—*Measurements and indices of the femur and tibia in* Shoshonius cooperi, *other fossil tarsiiforms, and some extant prosimians. Mean values are provided first, with ranges in parentheses. N (x,y,z) = sample sizes at proximal femora, distal femora, and tibiae, respectively. Femoral robusticity = (100)(femoral midshaft anteroposterior diameter + femoral midshaft mediolateral diameter)/femoral length. Other femoral measurements are defined in Dagosto and Schmid (1996). Distal tibial measurements are defined in Dagosto (1985).*

Taxon	N (x,y,z)	Lesser trochanter		Femoral neck	
		Projection	Angle	Length 1	Angle
Shoshonius cooperi	3, 1, 2	77.2	30	162.0 (153.8–170.1)	67 (63–70)
Hemiacodon gracilis	3, 1, 1	42.8	23 (20–27)	129.1	73.5 (72–75)
USNM 336187	1, 0, 0	69.7	20	137.6	74
?Omomys	1, 1, 3	38.9	12	129.3	71
Necrolemur sp.	1, 0, 1		47	179.2	65
Microchoerus sp.	1, 1, 0	72.7			
Leaper/quadrupeds					
Microcebus murinus	6, 14, 18	65.5 (38.3–88.9)	17 (9–23)	168.2 (142.3–193.2)	68 (65–75)
Cheirogaleus medius	3, 3, 3	62.1 (64.1–66.6)	11 (9–13)	174.4 (170.0–178.8)	62 (63–68)
Cheirogaleus major	6, 7, 7	62.1 (52.0–70.5)	16 (11–19)	183.0 (174.7–193.5)	64 (59–71)
Otolemur crassicaudatus	6, 6, 5	80.3 (70.3–93.0)	13 (8–16)	138.9 (120.1–154.2)	70.8 (65–76)
Otolemur garnetti	3, 6, 6	67.3 (57.5–79.8)	9 (5–14)	126.9 (122.0–130.3)	71.7 (65–80)
Galagoides demidovii	4, 4, 4	69.2 (60.3–78.7)	11 (7–14)	143.1 (127.0–154.1)	73 (67–79)
Specialized leapers					
Galago moholi	5, 5, 5	55.6 (52.2–66.9)	12 (10–15)	134.6 (119.4–152.7)	74.2 (72–80)
Galago senegalensis	3, 1, 2	62 (46–74.4)	11 (8–14)	141.8 (137.9–144.1)	74 (66–83)
Galago gallarum	5, 5, 4	64.6 (54.9–79.2)	8 (5–13)	153.6 (136.2–174.3)	77.5 (68–81)
Tarsius syrichta	6, 11, 6	79.3 (69.4–90.9)	9 (6–13)	152.2 (149.0–161.6)	78 (67–88)
Tarsius bancanus	4, 7, 7	69 (42.6–86.8)	10 (8–12)	149.0 (140.7–157.8)	71 (68–76)

rim (Fig. 6, 8). The ratio of condylar depth (anteroposterior dimension) to bicondylar width equals 111 in *Shoshonius*. Like *Hemiacodon*, *Shoshonius* compares best with specialized leapers such as *Tarsius, Galago*, and *Avahi* in this feature (Dagosto, 1993). As in extant frequent leapers, the patellar groove projects further anteriorly than the femoral shaft (Rose and Walker, 1985; Anemone, 1990, 1993). Unlike specialized leapers, however, the medial epicondyle exhibits only a slight anterior bulge and the distal articular surface of the medial epicondyle is only slightly indented (Dagosto, 1993). In these aspects of condylar shape, *Shoshonius* resembles *Hemiacodon* and *Microchoerus* and differs from tarsiers and galagos.

The femur of *Shoshonius* shares some features with extant specialized small-bodied leapers like the semicylindrical femoral head, the relatively perpendicular and short femoral neck, the enlarged, anteriorly prominent greater trochanter, the

Table 9.—*Extended.*

Fossa length	Femoral shaft ap/ml	Femoral robusticity	Humeral ap*ml/ femoral ap*ml	Lateral condyle height	Tibia Rotation	Tibia Distal ap/ml
112.7	87.4	12.2	70.1	111.5	15.5	117
(96.5–128.8)					(13–18)	(116.3–117.6)
115				116		120.6
113.3						
101.7				108.9	16	125.3
					(12–21)	(118.2–131.3)
152.2					20	129.2
107.8				>99		
132.3	105.7	12.8	77	98.9	29.3	134.8
(119.4–148)	(90.1–118.6)	(11.2–13.9)	(67–96)	(84.6–113.1)	(22–36)	(115–160)
137.8	100.9	13.5	86.4	90.6	31	131.5
(130.3–145)	(91.8–107.3)	(12.7–15.0)	(73.1–93.3)	(87.3–96.0)	(30–33)	(114–161)
125.2	106.6	13.6	93.1	98.5	32	125.1
(106.9–143)	(99.5–112.5)	(12.8–14.5)	(79.3–102.4)	(91.3–104.0)	(20–44)	(115.3–144.0)
101.0	99.7	12.2	71	102.5	28.8	123.5
(77.0–113.2)	(94–105)	(11.6–13.3)	(69.4–72.6)	(99.3–107.5)	(25–34)	(121.0–126.1)
89.8	97.7	12.3	71.7	97	34	112.1
(73.8–101.5)	(84–112)	(10.9–13.3)	(60.6–77.6)	(91.9–102.1)		(103.8–122.6)
91.8	110	11	67	105	21.6	126.6
(80.7–105.8)	(93–120)	(10.3–11.5)	(57–74)	(98.5–111)	(15–28)	(105.1–162.7)
84.5	121	11.2	50.7	111.8	23	115.9
(71.9–90.0)	(112–127)	(10.7–11.7)	(43–68)	(107.7–115.3)	(15–31)	(107.7–124.3)
94.3	119	11.6		112.7	20	135
(88.1–99.5)						(131.6–138.5)
94.9	112	10.8	52.2	114.4	21.5	100.4
(92.9–99.7)	(103–122)	(10.5–11.6)	(44–64)	(110.7–117.5)	(19–25)	(97.7–104.5)
97.5	114.1	9.3	74	116.3	14	104.9
(84.4–108.7)	(93.4–124.5)	(8.8–10.0)	(67–80)	(106.4–130.5)	(10–20)	(100.0–109.3)
98.5	124.9	9.2	74	118.5	18	117.2
(91.6–108.3)	(109–147)	(9.2–9.3)	(64–88)	(113.1–124.4)	(15–21)	(114.2–120.2)

short intertrochanteric fossa, and the deep knee. However, it differs from specialized leapers in its relatively short and robust femur, and the fact that the femoral shaft is broader mediolaterally than anteroposteriorly.

Tibia.—CM 69757 is a right tibia complete from the distal joint surface up to the tibial tuberosity (Fig. 9). It exhibits a marked anteroposterior S-shaped curvature, much greater than in *Tarsius*. The cnemial crest is prominent in *Shoshonius*, showing a height to midshaft height ratio of 1.71. The cnemial crest extends down about 15% of the estimated length of the tibia. In contrast to *Tarsius*, the tibia is not fused to the fibula. The bones were, however, in relatively close contact as demonstrated by the proximodistally extensive (approximately 25–35% of tibial length) tibiofibular scar. This degree of tibiofibular apposition is similar to that reported for the early Eocene anaptomorphine omomyid *Absa-*

Fig. 8.—Distal femora of extant prosimians and *Shoshonius* in distal view. From left to right, specimens illustrated are as follows: *Tarsius syrichta* (FMNH 142007), *Cheirogaleus medius* (FMNH 57521), and *Shoshonius cooperi* (CM 69764). Femora are scaled to the same mediolateral width. Note the anteroposterior depth of the knee in *Tarsius* and *Shoshonius*.

rokius (Covert and Hamrick, 1993) but is much greater than that in at least some middle Eocene omomyids from the Bridger Formation (Dagosto, 1985).

The talar facet is slightly longer than wide (Table 9), only moderately grooved, and its anterior and posterior edges are parallel. The tibial malleolus is long, pyramidally shaped, and rotated only 15° from a parasagittal plane. An anterior process is present. The groove for tibialis posterior courses across the posterior edge of the malleolus. In all of these features, *Shoshonius* is quite similar to other North American omomyids for which the relevant anatomy is known (Dagosto, 1985; Covert and Hamrick, 1993). *Necrolemur* differs in having a more highly grooved articular surface for the talus and a tibialis groove that curves around the medial edge of the malleolus (Dagosto, 1985).

Talus.—Three tali of *Shoshonius* were recovered (Fig. 10). The talus of *Shoshonius* is much like those of other omomyids. It exhibits a long talar neck, a high talar body, and a trochlea that is longer than wide (Table 10; Fig. 10). In these proportions, it is much like nonlorisine strepsirhine primates and other tarsiiforms, with the notable exceptions of *Necrolemur*, which has a short talar neck, and *Tarsius*, which is distinguished by its short talar neck and low body (Godinot and Dagosto, 1983). The posterior trochlear shelf is fairly prominent, a feature in which *Shoshonius* more closely resembles anaptomorphine omomyids than other omomyines (Gebo, 1988). As in other haplorhines, the groove for the tendon of flexor tibialis is centrally positioned relative to the tibial facet, and the fibular articulation is steep-sided and ends in a short process plantarly (Beard et al., 1988). The medial tibial facet extends to the plantar edge of the body. The talar head is much wider than high, suggesting considerable abduction/adduction movement at the transverse tarsal joint.

The talus of *Shoshonius*, like those of other omomyids, is distinguished from *Necrolemur* (Godinot and Dagosto, 1983) by its longer neck, lower body, and smaller posterior trochlear shelf. *Shoshonius* is also markedly different from *Tarsius* in its possession of a long talar neck, a round talar head, and its long, nonwedged trochlear body (Gebo, 1988). No features of the talus clearly distinguish extant vertical clingers and leapers from leaper/quadrupeds.

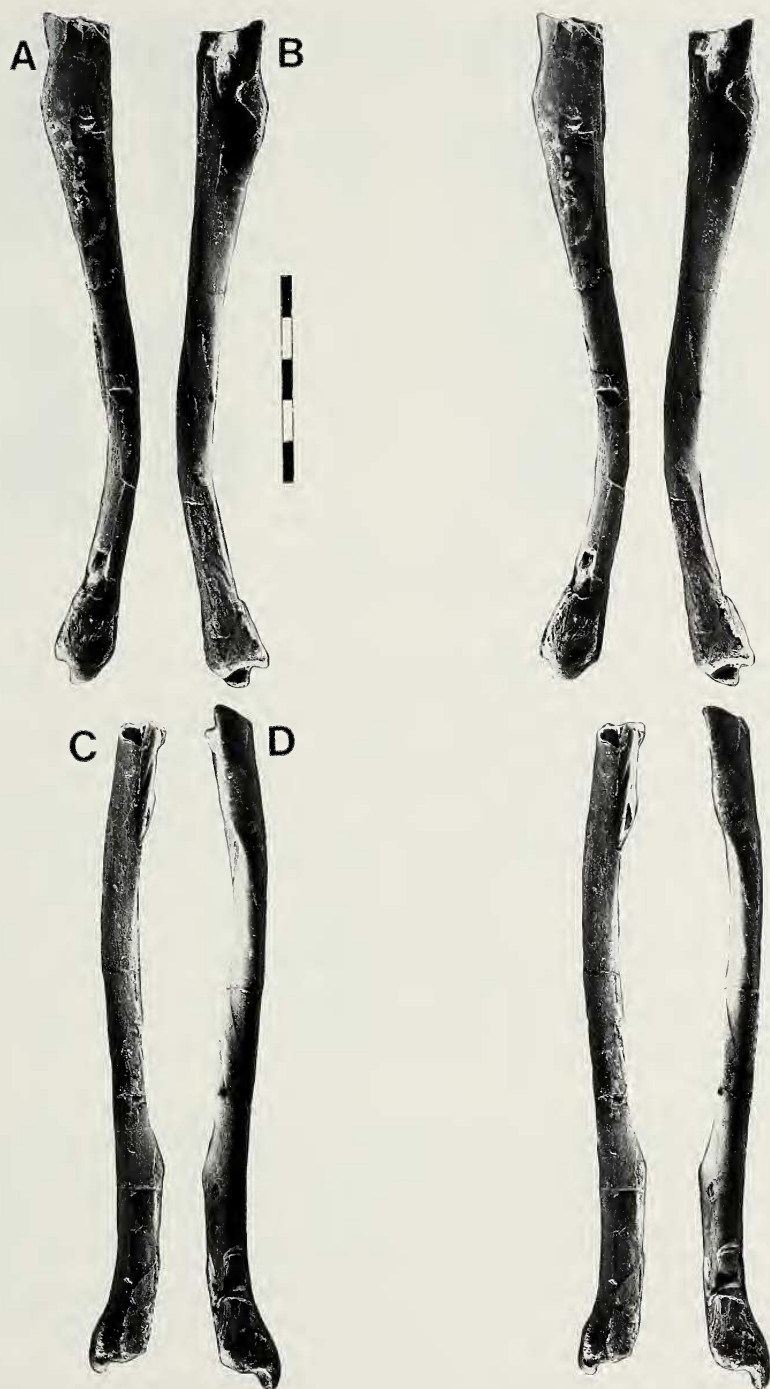*Calcaneus.*—The calcaneus of *Shoshonius* is very similar to those of other

Fig. 9.—Right tibia of *Shoshonius cooperi* (CM 69757) in medial (A), lateral (B), posterior (C), and anterior (D) views. All views are stereopairs. Specimen is complete aside from the missing proximal end and the adjacent part of the shaft. Note the proximodistal extent of tibiofibular apposition. Scale = 10 mm.
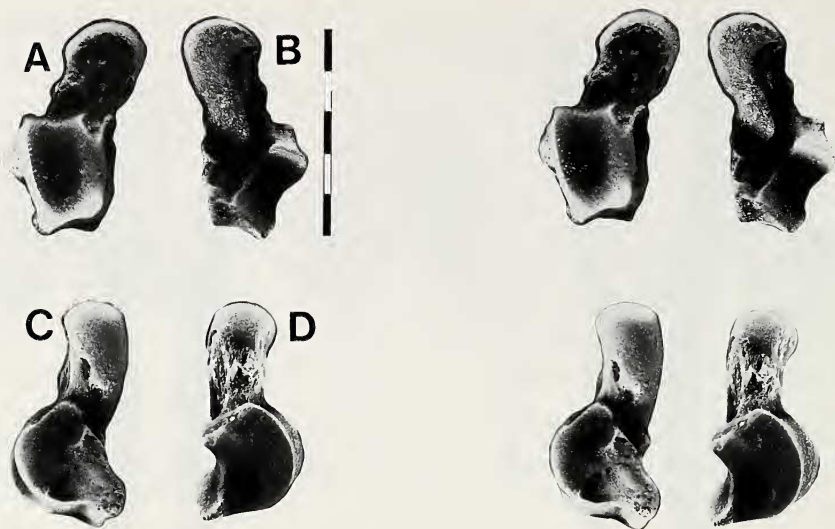
Fig. 10.—Left talus of *Shoshonius cooperi* (CM 67297) in dorsal (A), plantar (B), medial (C), and lateral (D) views. All views are stereopairs. Scale = 5 mm.

omomyines and anaptomorphines (Fig. 11). The proportions of the proximal (heel), middle (posterior talar facet), and distal regions of the calcaneus relative to total length do not distinguish *Shoshonius* from other North American omomyids (Table 11; Gebo, 1988). *Necrolemur, Microchoerus,* and *Tarsius* differ from *Shoshonius* (and other omomyids) in showing greater anterior elongation of the calcaneus (Schmid 1979; Gebo, 1988). *Shoshonius* and other omomyids also differ from *Tarsius* in several other ways. The peroneal tubercle is more anteriorly located in omomyids than in *Tarsius*. The calcaneocuboid joint of *Tarsius* is nearly as long as wide and is flat, lacking the well-developed pivot typical of other prosimian primates, including omomyids (Jouffroy et al., 1984; Gebo, 1987a). No features of the calcaneus clearly distinguish extant leaper/quadrupeds from VCLs. Although *Otolemur* has a relatively shorter anterior calcaneus than *Galago, G. demidovii* has an extremely elongated anterior calcaneus that is comparable to *Tarsius* (Jouffroy et al., 1984; Jouffroy and Gunther, 1985; Berge and Jouffroy, 1986).

First Metatarsal.—The proximal end of the first metatarsal of *Shoshonius* (Fig. 12) is very similar to that of *Hemiacodon* and other omomyids (Simpson, 1940; Szalay and Dagosto, 1988). *Shoshonius* and *Hemiacodon* both possess proximodistally long and dorsoplantarly tall peroneal tubercles that are unreduced, in contrast to the smaller peroneal tubercle of *Tarsius* (Table 12:c/d and h/g; Fig. 13). The great dorsoplantar height and mediolateral narrowness of the omomyid peroneal tubercle (Table 12:a/b; Fig. 13) contrasts with the dorsoplantarly shallower and mediolaterally broader peroneal tubercles of adapids (Fig. 14:a, e). In omomyids, the base of the peroneal tubercle is located in the midline, transverse to the proximal joint surface (Fig. 14:a). The peroneal tubercle is dorsoplantarly deep, mediolaterally narrow, flat on its medial and lateral sides, and rounded along its end. In adapids the peroneal tubercle is more nearly conical in appearance, being rough and irregular mediolaterally, and it begins off to one side and twists to a point. Further, the amount of bone lateral to the articular facet is much greater

Table 10.—*Measurements and indices of the talus in* Shoshonius cooperi, *other fossil tarsiiforms, and some extant prosimians. Mean values are provided first, with ranges in parentheses. Measurements are defined in Gebo (1988) and Gebo et al. (1991).*

Taxon	n	Trochlea width/length	Neck length/ total length	Talar head width/height	Body height/ trochlea width
Shoshonius cooperi	3	73.2	52.4	114.5	115.8
		(70.1–79.2)	(49.6–55.1)	(101.6–137.5)	(113.4–116.2)
?Hemiacodon	6	75.4	51.2	122.3	110
		(67.6–82.0)	(48.1–56.7)	(111.7–132.9)	(95.7–118.4)
?Omomys	8	82	50.8	124.3	107.3
		(74.9–91.4)	(48.6–53.5)	(118.1–135.4)	(98.4–118.8)
Washakius	1	66.1	52.4		117.7
Tetonius	3	74.7	54.9		116.5
		(66.7–78.7)	(53.8–56.7)		(115–118)
Absarokius	1	100	53.7		90.5
Necrolemur	1	82.2	44.9	112.2	110.1
Leaper/quadrupeds					
Microcebus murinus	19	74.7	50.2	116.2	113.5
		(64.0–90.9)	(40.6–58.8)	(75.0–140.5)	(100.0–135.5)
Cheirogaleus medius	5	71.9	48.7	126.3	101.3
		(66.7–78.1)	(45.9–54.9)		(96.5–103.8)
Cheirogaleus major	7	72.2	50.4	130.8	114
		(63.0–76.6)	(47.8–55.2)	(120.0–137.7)	(105.6–123.5)
Otolemur crassicaudatus	4	64.3	52.6	120.2	130.4
		(52.4–74.7)	(47.7–58.6)	(115.8–126.0)	(112.9–152.3)
Otolemur garnetti	7	65.9	49.6	119.8	124.9
		(58.1–82.4)	(45.8–55.8)	(110.2–125.0)	(113.3–139.5)
Galagoides demidovii	10	73.5	50.1	119.9	107.2
		(61.8–91.5)	(43.7–55.4)	(114.3–124.9)	(94.8–119.0)
Specialized leapers					
Galago moholi	9	76.4	52.9	119.2	102.5
		(67.4–89.5)	(50.0–54.8)	(111.8–125.0)	(88.2–112.9)
Galago senegalensis	6	78.7	52.5	124.7	106.1
		(68.2–88.1)	(44.3–57.1)	(124.1–125.2)	(88.9–123.3)
Galago gallarum	2	69.5	52.2	104.3	109.5
		(64.6–74.5)	(50.0–54.3)	(86.8–121.8)	(102.9–116.1)
Tarsius syrichta	9	88.9	48.8	118.1	74.7
		(71.4–103.8)	(39.8–61.4)	(114.3–123.9)	(67.5–87.1)
Tarsius bancanus	5	91.5	49.2	123.8	79.8
		(83.8–110.8)	(45.1–54.1)	(122.7–125.0)	(67.6–96.2)

in adapids than in North American omomyids (Fig. 14:d). The shape of the joint surface also differs in the two groups. Part of the proximal articular surface of the first metatarsal wraps around the lateral surface of the peroneal tubercle and is obliquely oriented relative to the long axis of the joint surface in omomyids (Fig. 14:b). In adapids this surface is aligned mediolaterally. The joint surface in adapids also encompasses a much wider arc than that of omomyids (Fig. 14:c, f; Szalay and Dagosto, 1988).

DISCUSSION

Functional Anatomy and Locomotor Adaptations.—The rounded shape of the humeral head and its projection above the tuberosities implies a considerable amount of mobility at the shoulder (Gebo, 1987*b*). *Shoshonius* does not share the distally narrow, anteriorly inflated humeral head of VCL primates (Schmitt, 1996).
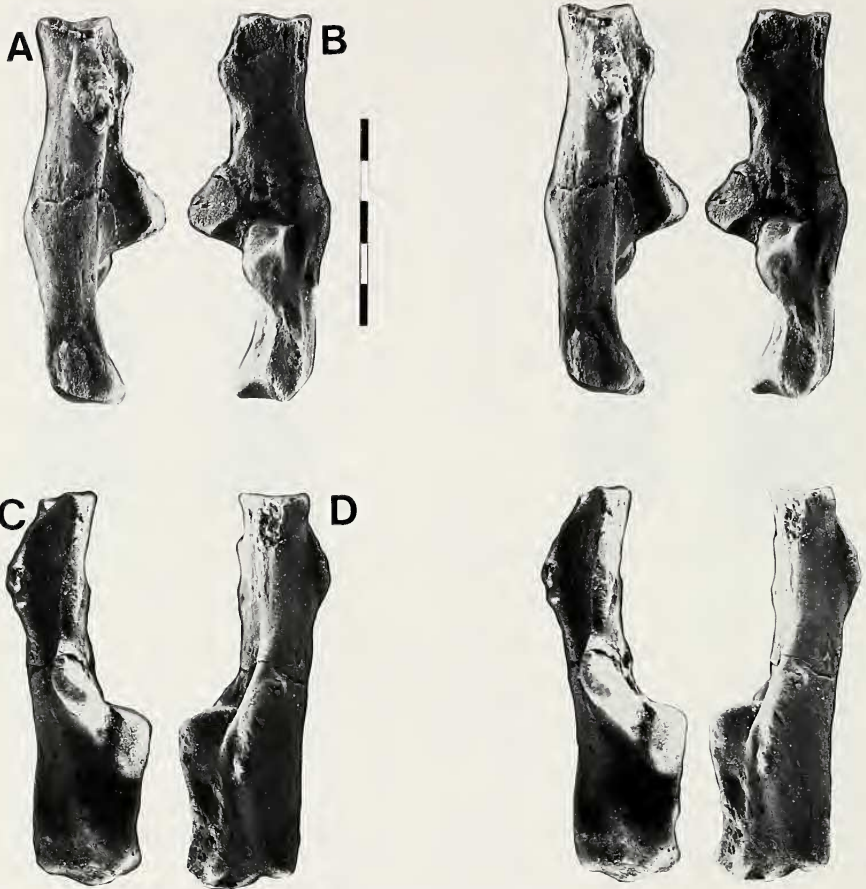
Fig. 11.—Right calcaneus of *Shoshonius cooperi* (CM 67299) in plantar (A), dorsal (B), medial (C), and lateral (D) views. All views are stereopairs. Scale = 5 mm.

The attachment areas for the muscles of the shoulder and forearm are larger than in most extant prosimian primates. The lesser tuberosity is very wide and prominent, suggesting a well-developed subscapularis, a muscle important for medial rotation of the humerus. Likewise, the deltopectoral crest and the brachial flange are wide and long relative to humeral length, suggesting well-developed and powerful deltoid, brachial, and brachioradialis muscles. The prominent medial ridge along the deltopectoral crest for latissimus dorsi suggests forceful adduction and medial rotation of the humerus. The medial and lateral epicondyles are very prominent, implying large forearm flexors and extensors, respectively.

The spherical shape of the capitulum on the distal humerus suggests extensive rotational abilities at the forearm and wrist. Likewise, the shallow olecranon fossa suggests that the forearm was never fully extended. The long, low trochlea on the distal humerus implies that clinging postures in which the elbow is highly flexed were not extensively utilized (Szalay and Dagosto, 1980).

The well-marked and frequently enlarged areas for muscular attachment, the overall robusticity of the humerus, and the mobility at the shoulder and elbow joints of *Shoshonius* imply that climbing and quadrupedalism were important

Table 11.—*Measurements and indices of the calcaneus in* Shoshonius cooperi, *other fossil tarsiiforms, and some extant prosimians. Mean values are provided first, with ranges in parentheses. Measurements are defined in Gebo (1988) and Gebo et al. (1991).*

Taxon	n	Heel length/ total length	Facet length/ total length	Anterior length/ total length	Cuboid facet width/height
Shoshonius cooperi	2	22.6 (21.9–23.4)	22.7 (22.3–23.1)	53.1 (52.9–53.4)	149.8 (146.8–152.9)
?Hemiacodon	10	28.7 (26.8–30.2)	19.6 (18.3–21.0)	52.3 (49.5–54.3)	125.3 (119.5–131.6)
?Omomys	8	26.3 (25.7–27.1)	18.5 (17.7–19.9)	52.6 (49.9–54.6)	134.2 (128.1–149.6)
Washakius	1	23.7	25.6	52.4	111.6
Absarokius	1	23.3	19.9	56.4	
Teilhardina	3	26.3 (25.7–26.8)	23.1 (20.3–26.5)	51.1 (47.1–54.1)	
Leaper/quadrupeds					
Microcebus murinus	18	19.3 (15.9–21.7)	18.9 (16.0–21.9)	61.4 (56.3–67.3)	104.1 (77.8–121.4)
Cheirogaleus medius	5	22.6 (18.7–25.3)	27.8 (21.1–31.0)	50.3 (46.5–52.3)	126.1 (116.5–133.3)
Cheirogaleus major	7	25.9 (20.0–29.8)	26.3 (24.1–28.6)	48.2 (46.1–50.0)	123.5 (103.7–155.0)
Otolemur crassicaudatus	6	19.7 (18.2–20.9)	16.8 (15.3–18.8)	64.7 (64.5–65.4)	118.7 (95.0–128.3)
Otolemur garnetti	7	20.2 (19.0–21.5)	15.3 (14.4–17.2)	64.6 (63.8–66.3)	116.7 (102.3–130.5)
Galagoides demidovii	10	12.6 (11.5–14.0)	10 (5.7–11.9)	77.2 (75.1–78.6)	115.3 (109.6–126.3)
Specialized leapers					
Galago moholi	9	16.2 (15.3–17.7)	11.7 (11.1–12.6)	72.2 (70.8–72.9)	124.5 (107.7–160.0)
Galago senegalensis	6	16.8 (13.5–18.2)	11.6 (9.3–12.8)	72.3 (70.5–76.2)	102.2 (97.6–106.7)
Galago gallarum	1	14.4	10.6	75	130.8
Tarsius syrichta	9	12.3 (11.1–13.6)	11.8 (10.2–12.9)	76.5 (76.2–77.4)	102.9 (82.3–125.1)
Tarsius bancanus	5	12.6 (11.2–13.9)	12.2 (11.6–12.9)	76.1 (76.1–76.9)	102.6 (81.9–121.7)

components of its locomotor repertoire. Extant specialized vertical clinging and leaping primates have humeri that are less heavily scarred by muscular attachments, and show modifications of the shoulder and elbow joint that are lacking in *Shoshonius*.

The semicylindrical femoral head indicates an emphasis on flexion and extension movements at the hip. The perpendicular angle of the femoral neck and the shortness of the head and neck also suggest a reduced emphasis on hip abduction. The anteriorly prominent greater trochanter reflects the increased size of the muscles governing knee extension. Likewise, the tall and narrow knee with its elevated and rounded lateral patellar rim and narrow patellar facet implies increased leverage for the quadriceps musculature. These features of *Shoshonius* are shared with frequently leaping primates.

As in leapers, the femur of *Shoshonius* is moderately long, but probably not as long relative to body size as in VCL galagos or tarsiers. The femoral shaft is more robust than in specialized VCL primates, and is particularly unusual in being
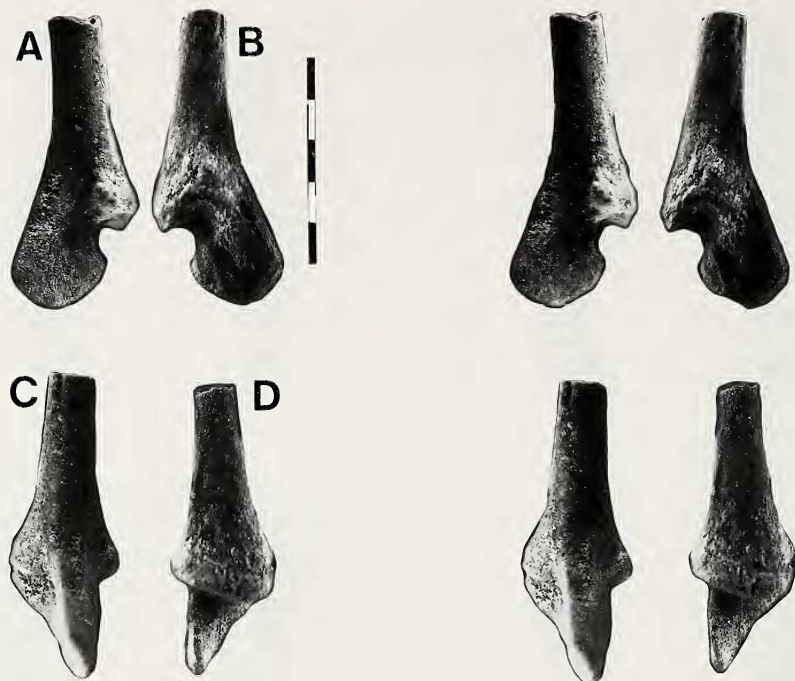
Fig. 12.—Right proximal first metatarsal of *Shoshonius cooperi* (CM 69754) in lateral (A), medial (B), plantar (C), and dorsal (D) views. All views are stereopairs. Scale = 5 mm.

wider mediolaterally than anteroposteriorly, suggesting more resistance to medio-laterally directed than anteroposteriorly directed bending forces. This arrangement is more typical of climbing than leaping primates (Burr et al., 1982).

The long, S-shaped tibia with its prominent cnemial crest, tightly apposed fib-ula, and only slightly medially rotated medial malleolus also imply that leaping

Table 12.—*Measurements and indices of first metatarsals (in mm). See Figure 13 for explanation of measurements.*

Measurement/index	Notharctus	Adapis	Leptadapis	Hemiacodon	Shoshonius
Mediolateral width of base of tubercle (a)	3.36	2.50	4.57	1.18	0.86
Mediolateral width of proximal metatarsal (b)	7.73	5.47	11.52	4.16	2.59
Dorsoplantar depth of tubercle (c)	9.81	5.75	11.79	6.28	3.30
Dorsoplantar depth of proximal metatarsal (d)	4.05	2.50	5.10	4.26	2.03
Dorsal length of metatarsal (e)	22.49	15.88	32.62	14.40	
Total length of metatarsal (f)	24.40	17.05	35.62	16.25	
Tubercle length (g)	5.34	2.99	5.80	4.59	2.36
Tubercle height (h)	4.37	2.22	4.89	4.50	2.23
a/b	43.5	45.7	43.8	28.4	33.2
c/d	41.3	43.5	43.3	67.8	61.8
e/f	92.2	93.1	91.6	88.6	
h/g	81.9	74.2	84.0	98.0	94.5
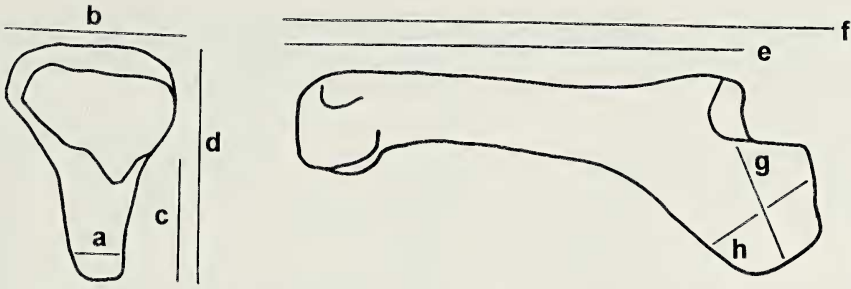
Fig. 13.—Measurements of the first metatarsal used to construct ratios provided in Table 12.

was an important component of the locomotor repertoire of *Shoshonius*. The long talar neck, the short and high talar body, the rectangular trochlea, the large posterior trochlear shelf, and elongated distal calcaneus all support an emphasis on flexion/extension movements at the upper ankle joint. In contrast, the large and round talar head, as well as the subtalar and calcaneocuboid joint surfaces, suggest a quite mobile tarsus and foot (Szalay, 1976; Dagosto, 1986; Gebo, 1988). The prominent peroneal tubercle on the first metatarsal implies an important role for peroneus longus in pedal grasping and/or a buttressing mechanism to deal with loads during leaping (Szalay and Dagosto, 1988).

Although *Shoshonius* has many characters of the hind limb (hip joint, knee joint, upper ankle joint) that suggest that leaping was an important part of its locomotor repertoire, living, small-bodied VCL primates like *Galago senegalensis, G. moholi*, and *Tarsius* show numerous specializations for leaping that are
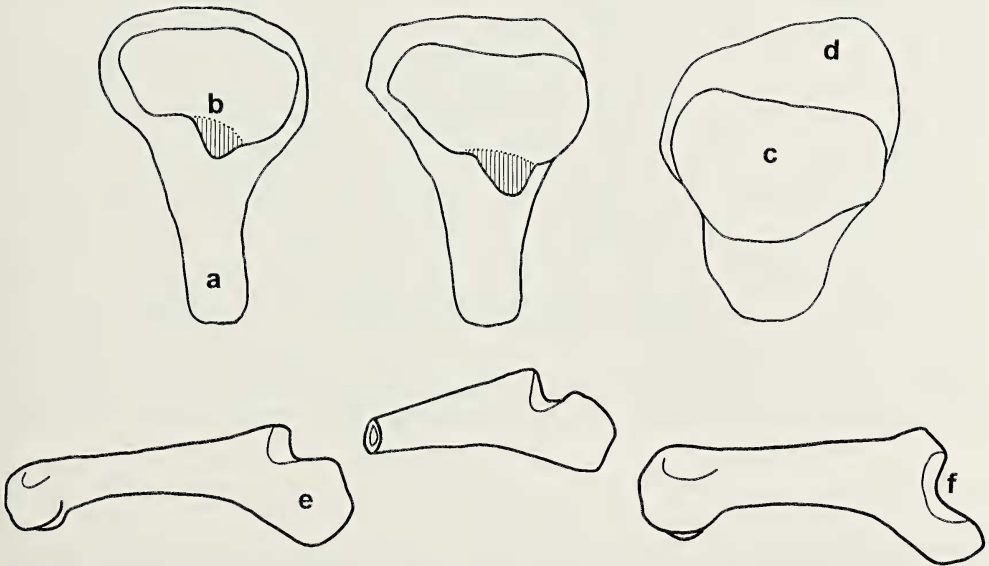
Fig. 14.—Proximal (top) and lateral (bottom) views of first metatarsals. Left to right: *Hemiacodon* (AMNH 12613), **Shoshonius** (CM 69754), and *Notharctus* (AMNH 11474). The letters a–f refer to features discussed in the text. The shaded area indicates the oblique direction of this region of the proximal articular facet in omomyids.

Table 13.—*Indices that distinguish leaper/quadrupeds* (Microcebus, Cheirogaleus, Otolemur, *and* Galagoides demidovii) *from specialized vertical clingers and leapers* (Tarsius, Galago senegalensis, G. gallarum, *and* G. moholi) *at* p < 0.05. *The* p *values are derived either from comparison of species means or individual specimens.*

Anatomical region	Source of data	Index	p values, species means	p values, individuals
Shoulder	Table 8	AP EXT	0.010	0.002
Shoulder	Table 8	INFW/PD CHORD	0.003	0.000
Elbow	Table 8	TH/TW	0.000	0.000
Elbow	Table 8	TW/AW	0.012	0.000
Femur	Table 9	Femoral shaft ap/ml	0.001	0.000
Femur	Table 9	Femoral robusticity	0.009	0.000
Humerus and femur	Table 6	HFI	0.000	0.000
Knee	Table 9	Lateral condyle height	0.000	0.000

absent in *Shoshonius*. Like other omomyid primates, *Shoshonius* shows significant differences from *Galago senegalensis, G. moholi,* and *Tarsius* in terms of limb proportions, shoulder joint shape, elbow joint shape, degree of forelimb muscularity, and calcaneal proportions. In these features, *Shoshonius* and other omomyids are more like small, extant strepsirhine primates in which quadrupedalism and climbing remain important parts of the locomotor repertoire. Our conclusions therefore echo and support the observations of Simpson (1940), Szalay (1976), and Gebo (1988), all of whom stressed the generalized, nontarsierlike nature of the postcranium of omomyids.

Eight of the indices considered in this analysis distinguish extant vertical clingers and leapers from leaper/quadrupeds (Table 13). In all of these indices except the height of the lateral femoral condyle relative to biepicondylar breadth, *Shoshonius* groups with the LQs and not with the VCLs. The variables used to construct these indices were subjected to a principal coordinates analysis (after the raw data were "adjusted" for size by subtraction of the geometric mean [Falsetti et al., 1993; Jungers et al., 1995]). Figure 15A shows the results. The first three axes account for 87% of the variation, and the correlation between the distances implied by the first three axes and the original distance matrix is 0.99, suggesting that these axes adequately characterize relationships among the taxa. Axis 1 (64%) separates the extant VCLs from the LQs. *Shoshonius* falls with the LQs on this axis, and the minimum spanning tree (Fig. 15A) shows that it is linked to members of the LQ group rather than any of the VCL group. A cluster analysis of this data is provided in Figure 15B. The cophenetic correlation of this tree with the original distance matrix is 0.79. Features that contribute most to the positive values of the VCLs on the first principal coordinate axis are femoral length, the ap diameter of the femoral shaft, and lateral condyle height (Table 14). The negative values of the LQs result from the width of the humeral head and

→

Fig. 15.—A. Principal coordinates analysis of variables contributing to indices separating leaper/quadrupeds from vertical clingers and leapers (see Table 13). The correlations between variables and axes is given in Table 14. The dotted line is the minimum spanning tree. B. A cluster analysis (UPGMA) of the same data. C. A principal components analysis of the raw data. Factor 1 (not shown) is likely a size vector; Factors 2 and 3 separate taxa in much the same way as the principal coordinates analysis. Eigenvectors are given in Table 14.
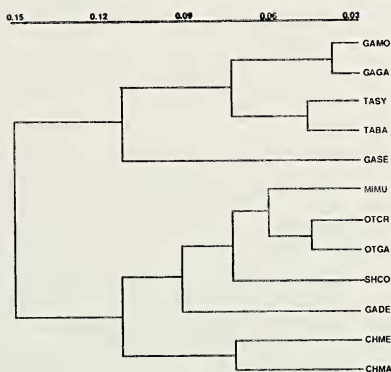
A **Principal Coordinates Analysis**
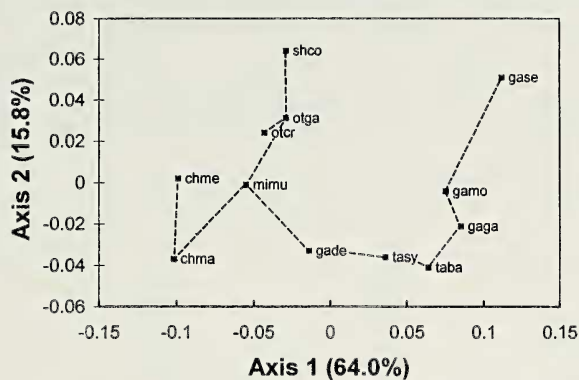
B **Cluster Analysis**
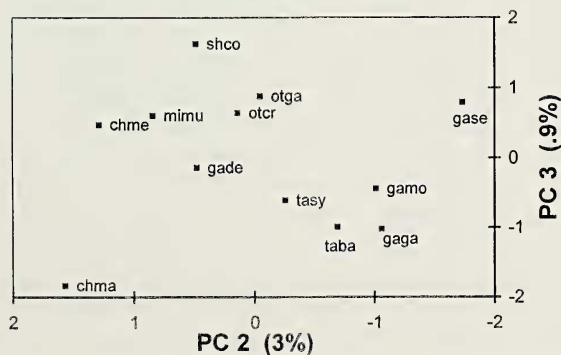

C **Principal Components Analysis**

Table 14.—*Relationship of variables to axes in principal coordinates and principal components analysis (Fig. 15). For the principal coordinates analysis, r is the correlation coefficient and p is given for those variables showing a significant (p < 0.05) correlation with the axes. For the principal components analysis, the loadings of the factors are given. Measurements are defined in Tables 8 and 9. Abbreviations are as follows: HUMAP, anteroposterior diameter of humeral midshaft; HUMML, mediolateral diameter of humeral midshaft; FL, femoral shaft length; FEMAP, anteroposterior diameter of femoral midshaft; FEMML, mediolateral diameter of femoral midshaft; BEW, biepicondylar width of femoral condyles; LCONHT, height of lateral femoral condyle.*

| Anatomical region | Measurement | Principal coordinates | | | | Principal components | |
| | | Axis 1 | | Axis 2 | | | |
		r	p	r	p	Factor 2	Factor 3
Humerus	HL	−0.029		0.262		0.003	0.090
Humerus	HUMAP	−0.447		0.036		0.045	0.002
Humerus	HUMML	−0.800	0.002	0.379		0.115	0.049
Shoulder	APEXT	0.031		−0.936	0.000	0.074	−0.293
Shoulder	INFW	−0.943	0.000	0.145		0.211	0.036
Shoulder	PD CHORD	−0.595	0.041	−0.425		0.090	−0.012
Elbow	AW	−0.789		−0.154		0.114	−0.006
Elbow	TH	0.120		−0.615	0.033	0.009	−0.038
Elbow	TW	−0.932	0.000	0.025		0.276	0.036
Femur	FL	0.965	0.000	−0.046		−0.411	−0.021
Femur	FEMAP	0.880	0.000	0.091		−0.281	−0.015
Femur	FEMML	0.374		0.835	0.001	−0.108	0.129
Knee	BEW	−0.048		0.451		0.004	0.041
Knee	LCONHT	0.096	0.000	0.138		−0.177	−0.009

width of the humeral trochlea. Both locomotor groups are widely spread on the second and third axes. A principal components analysis of raw data (no size "correction"; Fig. 15C) yields a similar positioning of taxa and relative loadings of variables on axes (Table 14).

Insofar as comparable elements exist, the postcranial morphology of *Shoshonius* is not significantly different from that of other North American anaptomorphine and omomyine omomyids. This similarity suggests that these other species were also leaper/quadrupeds rather than specialized vertical clingers and leapers, although in the absence of information on limb lengths it is difficult to distinguish small-bodied VCLs from LQs. The considerable similarity among North American omomyids in known postcranial elements suggests that the postcranium was relatively conservative in this group, despite its high species-level diversity and long stratigraphic range. Middle–late Eocene European microchoerids (*Necrolemur* and *Microchoerus*) differ from the North American forms in many anatomical features (Godinot and Dagosto, 1983; Dagosto, 1985; Dagosto and Schmid, 1996), some of which (lower humerofemoral and humerotibial indices, narrower humeral head, greatly elongated calcaneus) suggest a greater anatomical commitment to leaping than was the case in North American omomyids.

Phylogenetic Implications.—All omomyids and microchoerids for which the relevant anatomy is known are less derived postcranially than is *Tarsius*. Despite this fact, both omomyids and microchoerids share derived postcranial characters with tarsiers. For example, omomyids resemble tarsiers in having a short, perpendicularly oriented femoral neck, a semicylindrical femoral head that approaches the more fully cylindrical shape found in *Tarsius*, and a high knee (Dagosto and Schmid, 1996). On the other hand, microchoerids and tarsiers are derived in sharing distal tibiofibular fusion and anterior elongation of the calcaneus (Schmid,
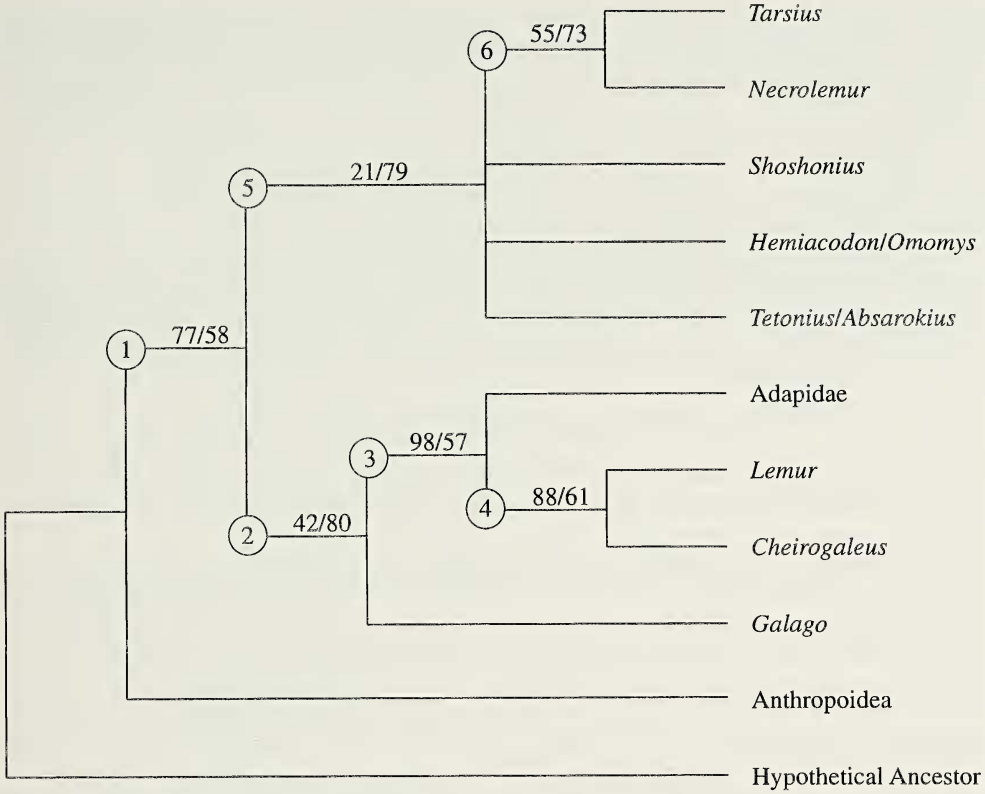
Fig. 16.—Strict consensus tree resulting from parsimony analyses of character-taxon matrix in Appendix 2 using PAUP 3.1.1 (Swofford, 1993). Characters were scaled for equal weighting regardless of number of character states. Characters 1, 2, 4, 5, 6, 9, 11, 13, 14, 20, 22, 25, 26 and 33 were treated as "ordered"; all other characters were treated as "unordered." The topology of the strict consensus tree was unaffected by separate analyses of postcranial characters alone and a combined dataset of both cranial and postcranial characters. Numerical values above stems of clades indicate percent frequency with which particular clades were supported in 1,000 bootstrapped trees. In each case, the number to the left indicates percent by which that clade was supported in bootstrapped trees derived from postcranial characters only, while the number to the right indicates percent by which that clade was supported in bootstrapped trees derived from the combined dataset.

Character transformations supporting each node are as follows (see Appendix 1 for description of character states): Node 1, Character 2 (0→1), Character 5 (0→2), Character 15 (0→1), Character 20 (0→1), Character 26 (0→1), Character 33 (0→1); Node 2, Character 12 (1→0), Character 13 (1→2), Character 14 (1→2), Character 17 (0→1), Character 18 (0→1), Character 25 (1→2), Character 26 (1→2), Character 34 (0→1), Character 44 (0→1); Node 3, Character 5 (2→1), Character 9 (1→0), Character 11 (1→0), Character 20 (1→2), Character 37 (0→1), Character 39 (0→1); Node 4, Character 19 (0→1), Character 23 (1→2), Character 52 (0→1); Node 5 (Tarsiiformes), Character 1 (1→0), Character 2 (1→2), Character 6 (0→1), Character 7 (0→1), Character 8 (0→1), Character 11 (1→2), Character 22 (1→2), Character 33 (1→2), Character 45 (0→1), Character 48 (0→1), Character 50 (0→1), Character 51 (0→1); Node 6, Character 11 (2→3), Character 15 (1→0), Character 16 (0→1), Character 21 (1→0), Character 22 (2→3), Character 24 (0→1), Character 30 (0→1), Character 38 (0→1), Character 42 (0→1).

1979; Dagosto, 1985; Gebo, 1987*a*). This pattern of crossing synapomorphies complicates attempts to reconstruct phylogenetic relationships and implies that at least some of these postcranial characters are the result of homoplasy (cf. Dagosto, 1985). Nevertheless, a recent phylogenetic analysis of primates based on postcranial characters (Dagosto and Gebo, 1994) supported the monophyly of Tarsiiformes (Tarsiidae + Omomyidae + Microchoeridae). This result agrees with some (Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994), but by no means all, recent phylogenetic analyses based on cranial anatomy.

A conflicting phylogenetic reconstruction holds that tarsiers share more recent common ancestry with anthropoids than they do with either omomyids or microchoerids (Cartmill and Kay, 1978; Cartmill, 1980; Cartmill et al., 1981; MacPhee and Cartmill, 1986; Ross, 1994; Kay et al., 1997). The monophyly of such a restricted tarsier–anthropoid clade rests largely on certain features of cranial anatomy, the homology of which has been fiercely contested (Simons and Rasmussen, 1989; Beard et al., 1991; Beard and MacPhee, 1994; MacPhee et al., 1995). Because the cranial anatomy of *Shoshonius* has played such a critical role in these debates, the addition of new data regarding the postcranial anatomy of this genus may help resolve the question.

We modified the postcranial dataset published by Dagosto and Gebo (1994: table 2) by incorporating new anatomical data for *Shoshonius*, adding additional strepsirhine taxa (*Cheirogaleus* and *Galago*), and including additional characters (Appendices 1, 2). Phylogenetic analysis of this enhanced postcranial dataset continues to support tarsiiform monophyly (Fig. 16). Omomyids, microchoerids, and tarsiers form a clade in all 14 of the most parsimonious trees found for postcranial features (220 steps), but this is not a robust link. The tarsiiform clade is evident in only 21% of bootstrapped trees. Trees only one step longer (0.4%) fail to support tarsiiform monophyly. Trees with *Galago* linked to *Tarsius* or within tarsiiforms are among the most parsimonious of these solutions, and are found in 39% of bootstrapped trees. Trees linking *Tarsius* to anthropoids, however, are considerably longer (34 additional steps or 15%), and this grouping is never encountered in bootstrapped trees.

Combining postcranial and cranial datasets (Beard and MacPhee, 1994) yields stronger support for tarsiiform monophyly. *Tarsius*, omomyids, and microchoerids form a clade in all 15 of the most parsimonious trees (336 steps), and this clade occurs in 79% of bootstrapped trees (Fig. 16). However, it takes only five additional steps (1.5%) to break apart the tarsiiform clade, although a *Tarsius* + *Necrolemur* clade is retained in the first 255 MPTs. Trees that fail to support a *Tarsius* + *Necrolemur* clade are at least 12 steps (3.6%) longer than the most parsimonious solutions. A strict tarsier–anthropoid clade requires 44 more steps (13%) and is never encountered in bootstrapped trees.

To summarize, considerable new information regarding the postcranial anatomy of *Shoshonius* corroborates a previous phylogenetic analysis of primates based on postcranial characters (Dagosto and Gebo, 1994). That is, although postcranial characters provide support for the monophyly of tarsiiforms, the degree of support for this clade is weak when postcranial characters alone form the basis for analysis. Small, vertical clinging and leaping strepsirhines such as *Galago* share numerous derived postcranial characters with *Tarsius*, thereby increasing homoplasy and reducing the level of character support for Tarsiiformes. However, the alternative hypothesis of a strict tarsier–anthropoid clade is clearly at odds with postcranial datasets. Given that studies of the cranial anatomy of *Shoshonius* and other

Eocene omomyids and microchoerids also support the monophyly of Tarsiiformes (Rosenberger, 1985; Beard et al., 1991; Beard and MacPhee, 1994), we conclude that tarsiers are more closely related to these extinct taxa than to living and fossil anthropoids.

ACKNOWLEDGMENTS

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APPENDIX 1

Character Descriptions

1. Femoral neck length short (0); medium (1); or long (2).[1-3]

2. Angle of femoral neck < 60° (0); 60–70° (1); or > 70° (2).[1-3]

3. Angle of lesser trochanter medial (0–30°) (0); or posterior (> 30°) (1).[2,3]

4. Size of third trochanter large (0); small (1); or crestlike or absent (2).[1-3]

5. Knee index < 90 (shallow knee) (0); 90–100 (1); or > 100 (deep knee) (2).[1,2]

6. Femoral head shape spherical (0); semicylindrical (1); or cylindrical (2).[1-3]

7. No anterior extension of greater trochanter (0); or greater trochanter extends anteriorly beyond proximal femoral shaft (1).[2,3]

8. Proximal femur not bent anteriorly (0); or bent anteriorly (1).[2,3]

9. Relative length of trochanteric fossa > 125 (long) (0); 110–125 (moderate) (1); or < 100 (very short) (2).[1-3]

10. "Intertrochanteric crest" absent (0); or present (1).[2,3]

11. Distal tibiofibular articulation unfused, synovial facet present (0); close apposition, facet present (1); close apposition, no facet (2); or fused (3).[1,2]

12. Distal surface of tibia square in outline (0); or triangular (1).[2,4]

13. No rotation of medial malleolus of tibia (0); slight medial rotation (1); or strong medial rotation (2).[1,2,4]

14. Medial malleolus of tibia flat (0); anteriorly convex, posteriorly flat (1); or all convex (2).[1,2,4]

15. Distal tibial shaft round in cross section (0); or anteroposteriorly compressed (1).[2]

16. Tibialis posterior groove located on medial side of malleolus (0); or on posterior side of malleolus (1).[2]

17. Flexor fibularis groove medially located with respect to trochlear articular surface (0); or laterally located (1).[2,5]

18. Facet for fibula on talus vertical (0); or laterally flaring (1).[2,5]

19. Trochlea on talus relatively short (0); or long (1).[2]

20. Posterior shelf on talus absent (0); present and small in size (1); or present and large in size (2).[1,2]

21. Relative length of talar neck < 100 (short) (0); or > 100 (long) (1).[2]

22. Degree of relative elongation of anterior part of calcaneus < 40 (short); 40–45 (moderate) (1); or > 45 (long).[1,2,6]

23. Peroneal tubercle on calcaneus distally located with respect to posterior talocalcaneal joint (0); located at joint (1); or located proximal to joint (2).[2]

24. Calcaneal bowing absent (0); or present (1).[2]

25. Trochlea on humerus conical in shape (0); cylindrical in shape, distal edge forms oblique angle to long axis of shaft (1); or cylindrical in shape, distal edge perpendicular to long axis of shaft (2).[1,2]

26. Dorsoepitrochlear pit on humerus present and conspicuous (0); small and shallow (1); or absent (2).[1,2]

27. Humeral head index infw/pdchord > 70 (0); < 70 (1).

28. Humeral head index ap/ext < 75 (0); > 75 (1).

29. Capitulum shape attenuated (0); round (1).

30. Relative hind limb length IMI or HFI > 60 (0); < 60 (1).

31. Relative height of humeral trochlea (index Th/TW) < 100 (0); > 100 (1).

32. Relative width of humeral trochlea (index TW/AW) > 45 (0); < 45 (1).

33. Length of navicular relative to width < 90 (short) (0); 100–150 (moderate) (1); or > 150 (long) (2).[1,2]

34. Facet for cuboid on navicular lateral in position (0); or plantar (1).[2,5]

35. Facet for first metatarsal on entocuneiform relatively flat, mediolaterally narrow, and restricted to distal end of entocuneiform (0); sellar-shaped and extensive (1); nonsellar-shaped and extensive.[2,7]

36. Auditory bulla separated from petrosal bone by a suture (0); bulla formed by petrosal (1).[8]

37. Ectotympanic expanded relative to ontogenetically early condition (0); ectotympanic not expanded and "ringlike" (1).[8]

38. External acoustic meatus not extended as a tube (0); tubelike (1).[8]

39. Annular bridge present and complete (0); present but incomplete (recessus dehiscence present) (1); annular bridge absent (2).[8]

40. Bony canals for proximal divisions of internal carotid artery absent (0); or present (1).[8]

41. Posterior carotid foramen posterolateral in position (0); posteromedial (1); or anterolateral (2).[8]

42. Suprameatal foramen absent (0); or present (1).[8]

43. Internal carotid artery unreduced in size (0); reduced, with function assumed by ascending pharyngeal artery (1); reduced, with function assumed by vertebrobasilar system or vessels other than the ascending pharyngeal (2).[8]

44. Parotic fissure present (0); or absent (1).[8]

45. Basioccipital flange overlapping bulla absent (0); or present (1).[8]

46. Apical aditus of anterior accessory cavity absent (0); or present (1).[8]

47. Central stem of basicranium broad (0); or narrow (1).[8]

48. Alisphenoid flange overlapping bulla trivial or absent (0); extensive (1).[8]

49. Postorbital septum absent (0); or present (1).[8]

50. Choanae broad in shape (0); or very narrow and "peaked" (1).[8]

51. Snout unreduced (0); or reduced (1).[8]

52. Toothcomb absent (0); or present (1).[8]

53. Postorbital bar absent (0); or present (1).[8]

[1] Multistate character treated as "ordered."
[2] Character from Dagosto and Gebo (1994:table 1).
[3] For further description of character, see Dagosto and Schmid (1996).
[4] For further description of character, see Dagosto (1985).
[5] For further description of character, see Beard et al. (1988).
[6] For further description of character, see Gebo (1988).
[7] For further description of character, see Szalay and Dagosto (1988).
[8] Character from Beard and MacPhee (1984).

APPENDIX 2

Taxon-Character Matrix Used in Parsimony Analysis

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Hypothetical ancestor   10000 00010  0?000 0?000 10000 ?0000 00000 00000 00000 00000 000
Galago                  02022 21020  11221 01101 13102 21101 11211 10020 10110 00000 011
Cheirogaleus            11001 00000  01221 01112 12202 20000 00011 11010 00110 00000 011
Adapidae                11001 00000  01221 01102 11102 20000 00011 11011 00010 00000 001
Lemur                   11001 00000  01221 01112 11202 20000 00111 11011 00010 00000 011
Anthropoidea            20110 0000(0,1) 10110 00010 11101 00000 00002 10021 10010 10010 001
Tarsius                 02002 21120  30110 10000 03111 21111 11201 10121 21001 11111 101
Necrolemur              2111? 01101  30110 10002 03111 1??01 00??? 10101 11001 00101 001
Shoshonius              02002 11110  20111 00001 12101 10010 00??? 10001 00001 01101 101
Hemiacodon/Omomys       02002 11110  20111 00001 12101 1???? 00101 ????? ????? ????? ?0?
Tetonius/Absarokius     ????? ?????  20111 00001 12101 1??0? 00??? 1???1 ??0?? ??101 101
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